



3 2044 105 172 092



HARVARD UNIVERSITY

LIBRARY

OF THE

GRAY HERBARIUM



Digitized by the Internet Archive
in 2014

U.S.
J-20.1
GH

GRAY HERBARIUM

OCT 01 1991

JOURNAL OF THE **ARNOLD ARBORETUM**



HARVARD UNIVERSITY SUPPLEMENTARY SERIES,
VOLUME 1

Despite the suspension of publication of the *Journal of the Arnold Arboretum* in 1990, we wish to continue supporting the Generic Flora of the Southeastern United States which has been published in the *Journal* since July 1958. Therefore we have initiated this supplementary series to be published as manuscripts become available. Each volume will be sold at cost.

Robert E. Cook
Director

This collection of contributions toward a Generic Flora of the Southeastern United States is the first volume in a Supplementary Series to the *Journal of the Arnold Arboretum*. It is our plan to continue the Series with additional volumes, each of which will contain other parts of the Generic Flora, a project that we have co-directed since 1981. The present five papers, numbers 136–140 of an anticipated 184 installments, were edited by us for botanical content and presentation, as well as to conform in format and style to other parts of the Generic Flora Project published over the past three decades in the *Journal of the Arnold Arboretum*. An ever-increasing amount of information about the plant resources of the world and numerous advances in the botanical sciences have together made more complex the task of reassessing and defining the taxonomic limits of plant genera. As a result, installment length has in some cases been increased to insure adequate coverage of the methods that have been used and that our authors employ to solve taxonomic problems presented by the seed plants of the Southeastern United States.

We are presently at work on a second set of five papers. These will comprise Volume 2 of the Supplementary Series.

Carroll E. Wood, Jr.
Norton G. Miller
2 August 1991

This book was composed by Norman F. Carlin and David Gladstein using the T_EX system for technical text developed by Donald E. Knuth. The body of the text is set in nine-point Herbarium, a type family adapted from Knuth's Computer Modern typefaces. The Metafont definitions of ten-point Computer Modern Roman, *Text Italic*, and **Bold Extended Roman** were modified to approximate the appearance of the text of previous parts of this series in the *Journal of the Arnold Arboretum*.

JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME 1

SUPPLEMENTARY SERIES

1991

THE GENERA OF BORAGINACEAE IN THE SOUTHEASTERN UNITED STATES¹

IHSAN A. AL-SHEHBAZ²

BORAGINACEAE A. L. de Jussieu, Gen. Pl. 128. 1789,
"Borragineae," nom. cons.

(BORAGE FAMILY)

Herbs, shrubs, trees, or rarely lianas, usually hispid to strigose or scabrous, rarely tomentose or glabrous; indumentum primarily of stout, eglandular, unicellular trichomes that often have silicified or calcified

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8717333 (Carroll E. Wood, Jr., principal investigator) and BSR-8716834 (Norton G. Miller, principal investigator). This treatment, 136th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. The references that I have not verified are marked with an asterisk.

I am most grateful to Carroll Wood and Norton Miller for their continuous support and help with many aspects of this paper, particularly their critical review of the manuscript. I am thankful to Norman Carlin for typing the manuscript; to James Miller, B. Verdcourt, and Mat Thulin for their views about the typification of *Cordia*; to Hollis Bedell, William Crins, Gordon Tucker, and Atef S. Soliman for their help with literature; to Gustavo Romero and Virgilio Viana for their help with Spanish and Portuguese, respectively; and to Jim R. Massey for sending the material of *Amsinckia*.

The illustrations were drawn by Rachel A. Wheeler (FIGURES 1-3) and Karen Stoutsenberger (FIGURES 4 and 5) under earlier grants. George K. Brizicky, Kenneth R. Robertson, and Carroll Wood prepared the material and supervised the illustrations. The drawings were made from preserved material variously collected by F. C. Craighead, A. & R. Wagner, Robertson, and Wood, as well as from herbarium specimens of the Arnold Arboretum and the Gray Herbarium.

²Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138. Present address: Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166-0299.

© President and Fellows of Harvard College, 1991.

Journal of the Arnold Arboretum, Supplementary Series 1: 1-169. 1991.

walls, [multicellular glandular trichomes rarely present]. Nodes unilacunar; xylem usually forming a ring, the vessels with simple or rarely reticulate perforation plates, the tracheids with narrowly bordered or simple pits; rays multiseriate or rarely uniseriate. Leaves simple, exstipulate, alternate or rarely opposite, entire or rarely lobed; stomata usually anomocytic; cystoliths and/or calcium oxalate crystals often present. Inflorescences bracteate or ebracteate, usually coiled, scorpioid (flowers borne on two sides of the rachis) or helicoid cymes (borne on one side of the rachis), uncoiled progressively and elongated at maturity, and forming racemelike or spikelike infructescences; the flowers rarely axillary and solitary. Flowers hypogynous, actinomorphic or zygomorphic (*Echium*), pentamerous [or tetramerous], perfect or imperfect and the plants then gynodioecious (*Echium*) [or dioecious (*Cordia*, *Rochefortia*)], homostylous or heterostylous. Calyx of [4] 5 (-8) free or basally connate, equal or unequal sepals, these rarely united to the tip, imbricate [or rarely valvate] in bud, usually persistent and often accrescent in fruit. Corolla sympetalous, regular or irregular, funnelform, salverform, tubular, campanulate, or rotate; lobes [4] 5 (-8), equal or rarely unequal, imbricate, convolute [or rarely valvate] in bud; throat with or without five faucal appendages (formices), these usually hairy or glandular, opposite corolla lobes, and formed by invaginations of the corolla tube from the outside. Androecium of epipetalous stamens as many as [rarely only 1] and alternate with corolla lobes; filaments inserted at the same or at different levels on the corolla tube, rarely appendiculate; anthers 4 sporangiate, 2 lobed, dehiscent by longitudinal slits, basifixed or basally dorsifixed, introrse, free to connivent [or connate into a cone around the style (*Halgania*)], with or without an apical appendage; pollen grains tricolporate, triporate, [polyporate, or polycolporate], spherical, oblate, prolate, or dumbbell shaped, bi- or trinucleate when shed. Glandular disc annular, subtending the base of and often confluent with ovary [rarely absent]. Gynoecium 2 carpellate [rarely 4 or 5 carpellate], syncarpous; ovary superior, sessile, unlobed or deeply 4 lobed, 2, 4 [or 10] loculate; ovules 1 per locule, anatropous or semi-anatropous, subbasal or axile [rarely pendulous], unitegmic, erect to subhorizontal, tenuinucellar or pseudocrassinucellar (*Heliotropium*), the endosperm development cellular or nuclear; styles 1 [or 2], terminal or gynobasic (arising between the distinct ovary lobes), simple, divided at apex into 2 or 4 branches; stigmas 1, 2, or 4, capitate to discoid, entire or 2-lobed, with or without an apical sterile cone. Fruit most commonly a schizocarp of four 1-seeded [or 2-seeded] nutlets (mericarps) that are variously attached to a gynobase, sometimes a fleshy or corky drupe with four 1-seeded or two 2-seeded stones, very rarely a berry or 1- or 2-seeded loculicidal capsule (*Wellstedtia*); gynobase (receptacle) flat, pyramidal, or columnar. Seeds without or rarely with an elaiosome; megagametophyte (embryo sac) of the Polygonum type; embryogeny of Chenopodiad or Asterad type; endosperm absent or scanty, rarely well developed and oily; embryo straight or curved; radicle short, the cotyledons plump or flat, plain or plicately

folded (*Cordia*), entire or deeply bifid to the base and appearing as 4 (*Amsinckia*). Base chromosome numbers 4–12. (Including Cordiaceae Dumort., Ehretiaceae Martius, nomina conservanda; Asperifoliaceae Reichenb., Buglossaceae Hoffmanns. & Link, Heliotropiaceae Schrader, Onosmataceae Horan., Scoriaceae Dulac, Sebestenaceae Friesen, Wellstediaceae (Pilger) Novák). TYPE GENUS: *Borago* L.

A family of about 130 genera and some 2500 species in five subfamilies and seven tribes (my compilation). The Boraginaceae are distributed throughout the tropical, subtropical, and temperate regions of the world. The centers of highest diversity in the North Temperate Zone are the Irano-Turanian and Mediterranean regions, and in the tropics are Central America and northern and central South America. The Boraginaceae are poorly developed in the colder regions, and, for example, Canada and Alaska combined contain no more than 60 indigenous and naturalized species. In contrast, Turkey has about 300 species, and Iran, Afghanistan, and Pakistan (combined) contain about 380 species. The richest concentration of genera is in Asia, where 41 of its 80 genera are endemic. There are 35 genera (12 endemic) in Europe, 30 (11 endemic) in North America, 30 (9 endemic) in Africa, 23 (10 endemic) in South America, and 10 (4 endemic) in Australia. The family includes some 46 monotypic genera and about 29 oligotypic genera (with 2 to 5 species each).

More than 50 percent of the species in the family belong to ten large genera: *Cordia* L. (320 species), *Heliotropium* L. (260), *Cryptantha* Lehm. ex G. Don (150), *Onosma* L. (150), *Tournefortia* L. (150), *Mysotis* L. (100), *Cynoglossum* L. (75), *Ehretia* L. (75), *Paracaryum* (DC.) Boiss. (including *Mattiastrum* (Boiss.) Brand) (70), and *Plagiobothrys* Fischer & Meyer (70). The Boraginaceae are represented in the southeastern United States by 18 genera and 47 species, of which 28 are indigenous. Small (1933) reported *Anchusa arvensis* (L.) Bieb. (as *Lycopsis arvensis* L.) from Tennessee, but the record has not been confirmed by subsequent authors, and I have not seen any material of the species from any of the Southeastern States. However, *Anchusa* L. is listed in the following key to the genera but is not treated for the Generic Flora.

The subfamilial classification of the Boraginaceae is based primarily on the nature of the attachment of the style to the ovary, the number of stylar branches, and the fruit type. In contrast, the tribal classification of the subfamily Boraginoideae rests primarily on the type of attachment of the nutlets to the gynobase and on the position of the attachment scars (areolae or cicatrices). However, the strict application of nutlet attachment as the basis of tribal delimitation can lead to artificial tribal boundaries and generic circumscriptions.

All except one of the five subfamilies of the Boraginaceae are represented in the New World. Subfamily Wellstedioideae Pilger is unigeneric, and *Wellstedia* Balf. f. includes three species, one each in Ethiopia; Socotra and Somalia; and Namibia and the Cape Province

(Hunt & Lebrun). The subfamily has been recognized by a few authors at the familial rank because *Wellstedia* has capsular fruits; peltate multicellular glands; and pendulous ovules. None of these characters is found in the Boraginaceae, but *Wellstedia* resembles the boraginaceous *Coldenia* L. (monotypic; eastern Asia) in pollen, wood anatomy, stomata, tetramery, and a few other features (Hunt) and is recognized by several authors (e.g., Cronquist (1981), Melchior) as representing a subfamily of the Boraginaceae.

Subfamily Cordioideae Gürke (trees or shrubs; style terminal, divided into four branches, each terminated by a stigma; ovary not lobed; fruit a drupe; cotyledons plicate; endosperm lacking) is almost exclusively tropical. It consists of 325 species in three genera, *Auxemma* Miers (two species, South America), *Patagonula* L. (two species, South America), and *Cordia*. The last is represented in the Southeast by both indigenous and cultivated species.

Subfamily Ehretioideae Gürke (trees, shrubs, or herbs; style terminal, divided into two branches, each terminated by a stigma; ovary not lobed; fruit a drupe; cotyledons flat; endosperm copious and fleshy, rarely obsolete) includes about 170 species in 11 tropical and subtropical genera. It is represented in the Southeastern States by three species of *Bourreria* P. Browne.

Subfamily Heliotropioideae Gürke (trees, shrubs, or herbs; style terminal, undivided; stigma 1; ovary not lobed or only slightly lobed above; fruit a drupe or schizocarp splitting at maturity into four nutlets; endosperm present or absent) is widespread in the tropics and in temperate regions. It includes about 415 species in six genera, of which *Ceballosia* Kunkel (Macaronesia), *Ixorhea* Fenzl (Argentina), and *Nogalia* Verdcourt (Somalia and Arabia) are monotypic. The remaining genera, *Argusia* Boehmer, *Heliotropium*, and *Tournefortia*, are represented in the Southeast by indigenous species.

Subfamily Boraginoideae (herbs or very rarely shrubs; style gynobasic; stigmas 1, 2, or 4; ovary deeply 4 lobed; fruit of 4 nutlets, endosperm lacking) is the largest in the Boraginaceae, is largely confined to the temperate and subtropical regions, and has been variously divided into several tribes. Of the seven tribes generally recognized, only the Trichodesmeae Zak. (three genera and 43 species; Africa, Asia, Australia) are confined to the Old World.

Tribe Eritrichieae (Bentham & Hooker) Gürke (including Asperugeae Zak., Craniospermeae (DC.) Popov, Cryptanthaeae Brand, Harpogonelleae Gürke, Heterocaryeae Zak., Rochelieae DC., Zoellerieae Gürke) (corolla blue or white, less commonly yellow or orange, the lobes imbricate in bud, the faucal appendages present or absent; style undivided; stigma 1; nutlets keeled dorsally, with small, elongated, submedial attachment scar; gynobase pyramidal or columnar) is the largest in the Boraginoideae and consists of about 36 genera and some 480 species.³

³Bentham & Hooker recognized the Eritrichieae as a subtribe of the Boragineae (as Borageae) and not as a tribe as many authors (e.g., Popov (1953), Riedl (1967)) have indicated. It appears that Gürke was the first to give the Eritrichieae tribal status.

It is distributed nearly equally in the Old and New Worlds and is represented in the southeastern United States by the genera *Amsinckia* Lehm., *Hackelia* Opiz, *Lappula* Moench, and *Plagiobothrys*.

The Lithospermeae (DC.) Gürke (including *Cerinthae* DC., *Echieae* DC.) (corolla yellow or orange, sometimes white, rarely blue or purple, the lobes imbricate in bud, the faucal appendages present or absent; style usually divided at the apex; stigmas 2 or rarely 4; nutlets erect or rarely bent, smooth or verrucose to tuberculate, not marginate, usually not strophiolate, the attachment scar broad, basal; gynobase flat) are the second largest tribe in the Boraginoideae. The tribe is distributed primarily in the temperate regions of the Northern Hemisphere. The group includes some 415 species in 24 genera, of which *Buglossoides* Moench, *Echium* L., *Lithospermum* L., and *Onosmodium* Michx. are represented in the southeastern United States.

The third largest and probably the most advanced tribe is the Cynoglosseae DC. (corolla blue or white, the lobes imbricate in bud, the faucal appendages usually well developed; style undivided; stigma 1; nutlets usually appendaged or winged, not strophiolate, widely spreading at base, the attachment scars small, not elongated, apical or subapical; gynobase pyramidal or columnar). The great majority (ca. 95 percent) of its 16 genera and nearly 250 species are distributed in the Old World. The tribe is represented in the Southeast by four species of *Cynoglossum*, only one of them indigenous.

The Boragineae (including *Anchuseae* DC.) (corolla blue, rarely white or yellow, the lobes imbricate in bud, the faucal appendages well developed; style usually simple; stigmas 1 or 2; nutlets with a basal annular rim, usually strophiolate, the attachment scar basal; gynobase flat, with broad cavities left by the strophioles) comprise approximately 160 species and 13 genera. The tribe is almost exclusively Eurasian and is represented in the New World, including the southeastern United States, by cultivated and naturalized plants of the genera *Borago* and *Symphytum* L.

The Trigonotideae (Popov) H. Riedl (corolla with or without faucal appendages, the lobes imbricate in bud; nutlets usually tetrahedral, usually not keeled dorsally, not strophiolate, the attachment scar basal or ventral below the middle; gynobase flat or pyramidal) include genera previously assigned tentatively to the Eritrichieae. The tribe includes some 16 genera and a little over 130 species, almost exclusively Eurasian. It is represented in North America by *Mertensia* Roth, of which one species is indigenous in the Southeast.

The unigeneric Myosotideae Reichenb. (corolla blue, white, or yellow, the lobes contorted in bud; style unbranched; stigma 1; nutlets smooth, usually laterally compressed, not keeled, the attachment scar very small, subbasal; gynobase flat) are nearly unique in the subfamily Boraginoideae in having corolla lobes with contorted aestivation. The type genus, *Myosotis*, is most highly diversified in Europe and adjacent Asia and in New Zealand. It includes both naturalized and indigenous species in the Southeastern States.

The subfamilial classification of the Boraginaceae is controversial, and several authors (e.g., Dahlgren (1977); Hutchinson (1969, 1973); Small (1933); Takhtajan (1987); Van Tieghem; Willis) have variously recognized the five subfamilies above as independent families. However, these subfamilies, which have been maintained by Cronquist (1981), Takhtajan (1969, 1980), and Thorne (1976, 1983), evidently are related to each other, are connected morphologically and palynologically by some intermediate genera, and are not treated as families by any recent students of the family. Johnston (1950) considered *Lepidocordia* Ducke (including *Antrophora* I. M. Johnston), which includes two species, one each in Nicaragua and Brazil, as an intermediate between the subfamilies Ehretioideae, to which it is now assigned, and the Heliotropioideae. Ivan M. Johnston (1951a) also indicated that the ehretiid *Coldenia* L., a monotypic genus that was considered by him to consist of many species now assigned to *Tiquilia* Persoon (Richardson, 1976, 1977), shows many evolutionary trends that illustrate the development of nutlets from a drupe, and that it shows more affinities to the Boraginoideae than any other genus of the Ehretioideae. In fact, Johnston (1950, p. 176) argued that "there are many reasons for believing that the original Boraginaceae were ehretiid in character and that from them have evolved in divergent lines of specialization the three other subfamilies, the Cordioideae, Heliotropioideae, and Boraginoideae, and perhaps even the modern Hydrophllaceae also." On the basis of pollen morphology, floral vasculature, endosperm development, and certain aspects of the ovules and embryos, Di Fulvio (1978) suggested that the Heliotropioideae and Ehretioideae are very closely related to each other, and that Hutchinson's (1973) placement of these subfamilies in two unrelated orders is unwarranted.

The tribal classification of the Boraginoideae was refined in the cumulative works of Johnston (particularly 1924b, 1925a, 1953a, 1954a, 1954b). The tribes of earlier authors (e.g., Bentham & Hooker, De Candolle) are now recognized as subfamilies. Johnston (1924b) recognized four tribes and considered the Lithospermeae to be basal in the Boraginoideae, the Eritrichieae to be intermediate between the first and the Cynoglosseae, and the Boragineae to be an off-shoot of the Lithospermeae. He relied heavily on the type of attachment of nutlets to the gynobase, particularly in assigning genera to tribes and in determining phylogenetic trends in the Boraginoideae. Similar conclusions regarding the tribal relationships within this subfamily have been reached by Al-Nowaihi *et al.* Recent students of the Boraginaceae, however, are of the opinion that Johnston's tribal boundaries are rather arbitrary and often blurred, and several additional tribes have since been recognized. Popov (1953), for example, accepted 13 tribes, but his tribal concept is rather narrow, and I have followed in the present treatment Riedl's (1967) classification, in which eight tribes have been accepted. Popov (1953) subdivided the Eritrichieae into five tribes and the Lithospermeae into three. His tribe Echieae is based largely on floral zygomorphy, but this feature has evolved independently several times within

the Boraginaceae, and some species of *Echiochilon* Desf. (17 species; Africa, Western Asia) of the Eritrichieae have bilabiate flowers (Johnston, 1957).

Riedl (1967, 1968) established the tribe Trigonotideae as an assemblage of genera that did not seem to fit well into the four tribes recognized by Johnston (1924b). Riedl (1968) considered the tribe to be basal in the Boraginoideae and indicated that it exhibits evolutionary trends from terminal to gynobasic styles, as well as the corresponding change in the position of ovules. He suggested that the Eritrichieae and the Lithospermeae probably originated from trigonotidoid ancestors similar to those of the subtribes Antiphytinae H. Riedl and Moltkiopsisinae H. Riedl, respectively. He also speculated that the Cynoglosseae evolved from the Trigonotideae and the Boragineae and Trichodesmeae from the Lithospermeae.

Although the tribes Cynoglosseae and Eritrichieae (as Cryptanthaeae) were monographed in great depth by Brand (1921, 1931, respectively), the very narrow generic concepts adopted by him and the numerous alterations proposed since make Brand's work out of date. Brand (1931) adopted the tribal name Cryptanthaeae instead of Eritrichieae on the basis of his erroneous judgment that *Eritrichium* is not a representative of the tribe. In contrast, the painstaking work of Johnston (1953a, 1953b, 1954a, 1954b) makes the Lithospermeae the best known tribe of the Boraginoideae.

Other controversial aspects of the Boraginaceae are the ordinal disposition and the nearest family relatives. Perhaps the least satisfactory treatment is Hutchinson's (1973), in which he placed the largely woody members in the Ehretiaceae in the order Verbenales and assigned the primarily herbaceous genera to the Boraginaceae of the unifamilial Boraginales. He derived the Verbenales from the Boraginales and the Boraginales from the Geraniales through the Polemoniales. He further considered the Ehretiaceae to be ancestral to the Verbenaceae St.-Hil. and the Boraginaceae as basal to the Labiatae Juss. (as Lamiaceae) Lindley). Other authors, who have divided the Boraginaceae into smaller families, have generally kept the segregate families together.

Cronquist (1969, 1981) and Thorne (1976) placed the Boraginaceae, along with the Labiatae and Verbenaceae, in the order Lamiales. They relied heavily on the presence of the usually gynobasic style, 2-carpellate gynoecium, 2-ovulate carpels, falsely 4-loculate ovary, and fruits usually consisting of four nutlets as basic features that show affinities between the three families. Dahlgren (1977, 1983) argues, however, that the Boraginaceae differ from the Labiatae and Verbenaceae in having usually alternate leaves, terete stems, usually actinomorphic flowers, and stamens equal in number to corolla lobes, and in often producing pyrrolizidine alkaloids and alkannins but not iridoid compounds. In contrast, the Labiatae and Verbenaceae have opposite leaves, usually square stems, zygomorphic flowers, stamens fewer than corolla lobes and produce iridoid compounds but not pyrrolizidine alkaloids or alkanin. Di Fulvio (1979) summarized the embryological data in these three

families and showed that the Boraginaceae have endosperm without a haustorium and embryos with a short suspensor. The Labiatae and Verbenaceae have endosperm with a haustorium and embryos with a long suspensor. Furthermore, Roth (1977) indicated that the nutlets of the Boraginaceae are readily distinguished from those of the Labiatae in the absence of slime cells and crystal cells.

The evidence at hand clearly favors the exclusion of the Boraginaceae from the Lamiales, and Thorne later (1983) placed the family along with others in a separate order, a disposition compatible with that of Takhtajan (1980) and of Dahlgren (1977, 1983). According to these authors, the apparent similarities in gynoecial and fruit characters evolved independently in the Boraginaceae from those of either the Labiatae or the Verbenaceae. Furthermore, the placement of the Boraginaceae with these two families created an artificial order, the circumscription of which neglects the significant morphological, embryological and chemical data. Cantino's cladistic analysis of the Lamiales shows that synapomorphies (shared derived characters) between this order and the Scrophulariales are stronger and more in number than those between the Lamiales and Boraginaceae.

Although differing in certain details, the systems of Dahlgren (1977, 1983), Melchior, Takhtajan (1980, 1987), and Thorne (1983) all agree on a close association between the Boraginaceae and the Hydrophyllaceae R. Br. and Lennoaceae Solms., in that these systems basically followed that of Bentham & Hooker in the placement of the first two families in the order Polemoniales. Bentham & Hooker, however, placed the Lennoaceae in the Ericales. Thorne (1983) followed Melchior in the placement of the Boraginaceae in a suborder of the Solanales, while Dahlgren (1977) and Dahlgren *et al.* followed Takhtajan (1969 and/or 1980) in including the Hoplestigmataceae Gilg in the suborder Boraginineae. The pollen data of Erdtman and Nowicke & Miller (1989) support such an association, particularly with the subfamily Ehretioideae, but Cronquist (1981) placed the Hoplestigmataceae in the Violales. The morphological characters that separate the Boraginaceae from the Labiatae support a close association between the Boraginaceae and Hydrophyllaceae. These two families are also similar in inflorescence type.

Chromosome numbers in the Boraginaceae are known for about 555 species (ca. 22 percent of the total) in 60 genera (my compilation). Nearly 78 percent of the species investigated are either exclusively diploid or include diploid and polyploid populations. The lowest chromosome number ($2n = 8$) in the family has been reported for three species of *Arnebia* Forsskål and for *Amsinckia lunaris* Macbr. (see Bolkhovskikh *et al.*), whereas the highest number ($2n = 144$) was recorded for *Symphytum cordatum* L. (Grau, 1968). Although the cytological data do not seem to support the infrafamilial classification of the family, they are somewhat useful in the delimitation and affinities of certain genera. For example, $x = 12$ is predominant in *Hackelia* and the related *Lappula*, while 8 is characteristic of *Echium*. Britton concluded

that the base chromosome number for the Boraginaceae is eight. As argued by Lewis, however, the base number is probably 12, which has been reported for 156 diploid species (my compilation), including 88 that belong to the genera *Cynoglossum*, *Hackelia*, *Mertensia*, and *Myosotis*. The base number 12 is somewhat common in the tribes Cynoglosseae, Eritrichieae, and Trigonotideae. Polyploidy apparently did not play a major role within the family; aneuploidy was probably more significant. The tropical and subtropical members of the family are the least studied cytologically and, of the approximately 575 species that belong to the genera *Bourreria*, *Cordia*, *Ehretia*, and *Tournefortia*, apparently only 34 have been surveyed.

Members of the Boraginaceae are pollinated primarily by insects, and numerous pollinators are listed in Knuth. Selfing is also common, particularly among the weedy taxa. Bat pollination has been observed in two species of *Cordia* (see Palacios-Chávez, under *Cordia* references). Hummingbird pollination was first reported in the family by Grant & Grant, who observed two species of the genus *Selasphorus* pollinating the yellow-flowered *Macromeria viridiflora* DC. var. *Thurberi* (A. Gray) I. M. Johnston. One species of *Macromeria* D. Don, *M. exserta* D. Don (Nayarit south into Oaxaca, Mexico), has the largest flowers in the Boraginaceae, with corollas up to 9 cm long and exserted stamens to 7 cm long (Johnston, 1954a).

Heterostyly (distylous type) has been documented in various species of *Amsinckia*, *Anchusa*, *Arnebia*, *Cordia*, *Cryptantha*, *Echioides* Ortega, *Lithodora* Griesb., *Lithospermum*, and *Paracaryum*, as well as in all species of *Pulmonaria* L. (Ganders, 1979; Philipp & Schou). Distyly is associated with self-incompatibility in all of these genera except *Amsinckia*, in which all distylous taxa are self-compatible. Dimorphism in size and/or shape of pollen grains has been observed in the distylous species of *Cordia* and *Lithospermum*. As in most distylous plants of other families, those of the Boraginaceae that have been studied genetically, particularly species of *Amsinckia*, have the short-styled morphs (thrum) heterozygous and the long-styled morphs (pin) homozygous recessive. However, in *Anchusa* a multiallelic incompatibility system, unlinked to the locus controlling floral dimorphism, has been suggested (Barrett). Species of *Anchusa* show considerable variation in style length, but the ratio of anther height to style length exhibits a bimodal pattern. In some species of *Cordia* the style of pin flowers surpasses the anthers only slightly, but in thrum flowers the stigmas and anthers are well separated. Thrum flowers are considerably larger than pin flowers in *Cordia Sebestena* L. and in *Lithospermum caroliniense* (J. F. Gmelin) MacM., but in species of other genera the pin and thrum flowers are about the same size.

Numerous species of the Boraginaceae have five faucal appendages (fornices) alternating with the stamens at the apex of the corolla throat. They often close the corolla throat and allow only insects with a long proboscis to reach the nectar at the base of the corolla tube. These

appendages, which are invaginations of the corolla, are sometimes colored differently from the rest of the corolla and therefore act as nectar guides.

Change in the color of a given flower during anthesis in species of certain genera, particularly *Mertensia* and *Myosotis*, is attributed to a change in hydrogen-ion concentration (pH) in the cell sap (Good). Casper & La Pine observed that in *Cryptantha humilis* (Greene) Payson the change in flower color from yellow to white is associated with a substantial reduction in pollen viability and stigma receptivity, as well as with a significant reduction of insect visitations.

Pollen morphology has been studied in numerous genera of the Boraginaceae. Erdtman was among the first to point out that the family is different palynologically from the Labiatae but similar to the Hydrophyllaceae. Johnston (1953a, 1953b, 1954a, 1954b) gave detailed accounts of the pollen of all genera of the Lithospermeae, and in the last reference he used pollen data in the first couplet of the key to the genera of the tribe. Pollen morphology has been found to be valuable in delimiting genera, e.g., *Pardoglossum* Barbier & Mathes from other members of the Cynoglosseae (Clarke *et al.*); in the infrageneric division of *Cordia* and *Tournefortia* (Nowicke & Ridgway and Nowicke & Skvarla, respectively; see under generic references); and in the separation of species and genera (Sahay). Some palynological differences between the subfamilies Cordioideae and Ehretioideae have been observed (Nowicke & Miller), and phylogenetic affinities between the subfamilies and tribes have been proposed (Ahn & Lee). Pollen in the family ranges from tricolporate (*Echium*) to 10-zonocolporate (*Borago*) or 12-heterocolporate (*Myosotis*), from isopolar (*Borago*) to heteropolar (*Lithospermum*), from isodiametric (*Amsinckia*) to prolate (*Heliotropium*) or dumbbell-shaped (*Lappula*). The diversity in pollen ornamentation, size, shape, and number of colpi is so great that general surveys (e.g., G. C. S. Clarke) should be consulted for a better understanding of the family.

Brewbaker suggested that the woody borages (Cordioideae and Ehretioideae), as well as *Heliotropium*, have binucleate pollen and that the Boraginoideae have trinucleate pollen. However, he surveyed only 19 genera of the family, and binucleate pollen has been found in *Heliotropium* and *Trichodesma* R. Br. (G. L. Davis).

Fossil pollen assigned to *Symphytum* and to *Cordia* and *Tournefortia* has been reported from the Miocene of Spain and the Marshall Islands (western Pacific), respectively (Muller). Pollen of *Tournefortia* from the Miocene of Mexico and Oligocene of Puerto Rico has also been reported (Graham & Jarzen). The Boraginaceae were diversified during the Late Miocene, and fossil nutlets of the extant genera *Cryptantha* and *Lithospermum* and of the extinct genera *Biorbia* Elias, *Eliasiana* Thomasson, *Prolappula* Thomasson, and *Prolithospermum* Elias have been found (Gabel). Johnston (1954a) gave a lengthy discussion of the position of *Prolithospermum* in relation to the evolution of members of the Lithospermeae. However, the fossil record of the family is far

from being adequate to provide grounds on which phylogenetic trends or speculations can be based.

Endosperm development in the Boraginaceae varies from nuclear (as in *Borago* and *Cynoglossum*) to cellular (*Coldenia*, *Ehretia*, *Myosotis*). In addition to these basic types, Svenson recognized three intermediate types that he described from *Anchusa* (as *Lycopsis*), *Echium*, and *Lappula*. The embryological data do not support the division of the Boraginaceae into four or five families (Di Fulvio, 1978, 1979; Khaleel, 1982, reference under *Cordia*). However, on the basis of presence of endosperm haustoria and pollen-tube callose, Cocucci suggested that the Heliotropiaceae (including the subfamilies Cordioideae, Ehretioideae, and Heliotropioideae) be placed in the Hydrophyllales, and the remainder of the Boraginaceae be assigned to the Polemoniales.

The distribution of pyrrolizidine alkaloids in the unrelated dicotyledonous families Ranunculaceae Juss., Leguminosae Juss. (Fabaceae Lindley), Apocynaceae Juss., Boraginaceae, and Compositae Giseke (Asteraceae Link) reflects convergent evolution (Gerschenzon & Mabry). Their presence in the Boraginaceae is unique within all orders in which the family has been placed. Within the family, the Heliotropioideae and all tribes of the Boraginoideae contain diverse kinds of these alkaloids, but subfamilies Cordioideae and Ehretioideae apparently do not produce these compounds. The pyrrolizidine alkaloids are potentially important in chemotaxonomic studies of individual genera but apparently are not very useful in assessing phylogenetic relationships at higher taxonomic levels.

The consumption of pyrrolizidine alkaloids by livestock and by humans (as tea, vegetables, medicine, and contaminated food) has caused a great deal of concern because of the hepatotoxic and carcinogenic effects of these compounds (Bull *et al.*; Smith & Culvenor; Wróbel). Alarming results were obtained from experiments in which animals developed chronic liver damage as a result of eating foods containing low concentrations of pyrrolizidine alkaloids (Smith & Culvenor).

Herbivores feeding on plants containing pyrrolizidine alkaloids are believed to convert these compounds into defensive substances. The alkaloids apparently are accumulated by the feeding larvae, but adults can also obtain them from nectar or from dead or wilting plants. Pyrrolizidine alkaloids are also accumulated by male butterflies of the subfamilies Danainae and Ithomiinae. Secretions from the hair pencils, the pheromone disseminating organs of these insects, contain dihydropyrrolizidine derivatives that are believed to act as aphrodisiac or flight arrestant pheromones in the female butterflies. It has also been suspected that the female butterflies use these alkaloids to locate larval food plants (Edgar & Culvenor; Edgar *et al.*).

On the basis of gas-chromatographic analysis of fatty acids of 39 species in 19 genera of the subfamilies Heliotropioideae and Boraginoideae, Tétényi proposed a basal position for the first and placed the Echieae, Eritrichieae, and Boragineae (as Anchuseae) in a position intermediate between the Lithospermeae and the advanced Cynoglosseae. Huizing

& Malingré, who studied the profiles of pyrrolizidine alkaloids and phenolic compounds of 20 species in 15 genera, reached conclusions similar to those of Tétényi but suggested a closer relationship between the Cynoglosseae and Heliotropioideae.

Although the Boraginaceae are highly diversified in the external morphology of their nutlets, the family is rather uniform in the anatomy of the pericarp. The Lithospermeae differs from the other tribes of the Boraginoideae in that the mesocarp consists of thickened, sclerified cells, instead of remaining parenchymatous. The outer layer of the pericarp consists of palisade-like sclereids and usually becomes multi-layered within the protuberances (e.g., wrinkles, hooks, appendages, bristles) of the nutlet. The core of such protuberances consists of elongated cells, the radial walls of which have pitted secondary walls with undulated thickenings, whereas the outer surface of these structures may become silicified and is usually covered with a very thick cuticle that extends into bristles or tubercles (Roth, 1977).

Fruits of the Boraginaceae are dispersed in a variety of ways. The corky nutlets of *Argusia* species and *Mertensia maritima* (L.) Gray, as well as of several coastal species of *Cordia*, are dispersed by sea. In *Patagonula* (2 species; South America) the fruiting calyx develops into conspicuous wings, and the fruits are apparently dispersed by wind (Good). Several species of *Cryptantha* regularly fail to produce four nutlets from a single flower, and the fruiting calyx, which detaches from the infructescence, is dispersed by wind (Casper & Wiens; Grau, 1983). The broadly winged fruits of some species of *Paracaryum* are also wind dispersed.

The presence of glochidiate appendages on the nutlets of several genera of the Eritrichieae (e.g., *Hackelia*, *Lappula*) and Cynoglosseae (e.g., *Cynoglossum*) are adaptations to dispersal by clinging to animal fur (and human clothing). Similar dispersal is achieved by the presence of hooks on the fruiting calyx, as in many species of *Myosotis*, or by the modification of the nutlet beak into a hook, as in *Ancistrocarya japonica* Maxim. (Johnston, 1954a).

In some species of *Myosotis* and many members of the tribe Boragineae an elaiosome (or caruncle) is produced at the base of the nutlet. The development of elaiosomes was studied by Baciú, who stated that these structures originate from the mesocarp by the considerable elongation of parenchymatous cells toward the gynobase. The elaiosomes store sugars, oils, and free fatty acids, including ricinolic acid. Ricinolic acid has been shown to trigger a strong collecting impulse in ants, but the presence of this acid has not been tested in genera such as *Symphytum* and *Pulmonaria* that produce elaiosomes (Bresinsky).

The fruits of many species of *Cordia* are eaten by mammals such as bats of the genus *Phyllonycteris* and monkeys of the genus *Semnopithecus*. The endocarps are dispersed for short distances. Nutlets of numerous species (e.g., those of *Heliotropium* and *Lithospermum*) are eaten by birds, and those that remain viable after passing through

the digestive tract can be transported for various distances from their original source.

The Boraginaceae are of relatively little economic value. Many genera include species that are cultivated as ornamentals (Ingram, 1961). These include *Anchusa* (alkanet), *Borago* (borage), *Cordia*, *Cynoglossum* (hound's tongue), *Echium* (viper's bugloss), *Heliotropium* (heliotrope), *Mertensia* (bluebell), *Myosotis* (forget-me-not), *Pulmonaria* (lungwort), and *Symphytum* (comfrey).

Several species of *Cordia* (e.g., *C. alliodora* (Ruíz & Pavón) Oken, *C. Gerascanthus* L., *C. trichotoma* (Vell.) Arrab. ex Steudel), as well as *Patagonula americana* L., are valuable timber trees in Central and South America. Their wood is used in construction and in making furniture, flooring, tool handles, and musical instruments. The fruits of several species (e.g., *C. Sebestena* L., *C. Myxa* L.) are edible.

The roots of many species of Boraginaceae, particularly in the genera *Alkanna* Tausch, *Anchusa*, *Arnebia*, *Cynoglossum*, *Echium*, *Lithospermum*, and *Onosma*, yield red to purple naphthaquinone dyes commonly known as alkannins. These dyes, especially those obtained from the European *Alkanna tuberculata* (Forsskål) Meikel (= *A. tinctoria* Tausch) and the eastern Asiatic *Lithospermum erythrorhizon* Sieb. & Zucc., were used by the early Romans and by the Japanese, respectively, as coloring agents for wood, medicine, cosmetics, and wines. Papageorgiou (1978) demonstrated that the alkannin esters of isovaleric, angelic, and dimethylacrylic acids have excellent wound-healing properties.

Several members of the family (e.g., *Borago*, *Symphytum*) have commonly been used as potherbs and for their medicinal and culinary values. Because of the presence of pyrrolizidine alkaloids and their potential hepatotoxic and carcinogenic effects, the use of these plants for such purposes has declined tremendously. Many species of the genera *Amsinckia*, *Echium*, and *Heliotropium* are noxious weeds, and cattle, horses, and swine feeding on large quantities of these plants develop lesions, ulcers, walking disorders, and severe liver damage (Kingsbury).

Species of numerous genera have been listed as having various medicinal attributes. The treatments of Ayensu, H. M. Burkill, Duke & Ayensu, Lewis & Elvin-Lewis, Moerman, Perry, Quisumbing, and Uphof should be consulted for leads.

REFERENCES:

- ADAMS, C. D. Flowering plants of Jamaica. 848 pp. Mona, Jamaica. 1972. [Boraginaceae, 616-626.]
- AHN, Y. M., & S. LEE. A palynotaxonomic study of the Korean Boraginaceae. Korean Jour. Pl. Taxon. 16: 199-215. 1986. [Eighteen species in 14 genera, including *Amsinckia*, *Cynoglossum*, *Hackelia*, *Lappula*, *Lithospermum*, *Mertensia*, *Myosotis*, *Symphytum*; light and scanning-electron microscopy.]
- ALAIN, Hno. Boraginaceae. In: Hno. LEÓN (J. S. SAUGET) & Hno. ALAIN (E. E. LIOGIER), Fl. Cuba 4: 252-278. 1957. [Forty-one species of *Cordia* recognized.]
- AL-NOWAIHI, A. S., S. F. KHALIFA, & K. HAMED. A contribution to the taxonomy of Boraginaceae. Phytologia 62: 107-125. 1987. [Thirty-three species

in 18 genera, including *Borago*, *Cordia*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lappula*, *Lithospermum*, *Lycopsis*, *Symphytum*; comparative morphology, floral anatomy, evolutionary trends, "phylogeny."]

ALTAMURA, L., M. COLASANTE, & G. D'AMATO. Numeri cromosomici per la flora Italiana: 1022-1036. *Inform. Bot. Ital.* 16: 261-270. 1984. [*Anchusa*, *Asperugo*, *Buglossoides*, *Cerinth*, *Cynoglossum*, *Echium*, *Heliotropium*, *Solenanthus*, 261-265.]

ALTSCHUL, S. VON R. Drugs and foods from little-known plants: Notes in Harvard University Herbaria. *Frontisp.* + xii + 366 pp. Cambridge, Massachusetts. 1973. [Boraginaceae, 237-243.]

ARISTEGUIETA, L. Familias y géneros de los árboles de Venezuela. 845 pp. Caracas. 1973. [Boraginaceae, 150-155; *Bourreria*, *Cordia*, *Lepidocordia*, *Rocheftoria*, *Tournefortia*.]

AVETISIAN, E. M. Morphologie der Mikrosporen der Boraginaceen. (In Russian.) *Trudi Bot. Inst. Armen. SSR* 10: 7-66. 1956.*

AYENSU, E. S. Medicinal plants of the West Indies. 282 pp. Algonac, Michigan. 1981. [Boraginaceae, 58-62; *Bourreria*, *Cordia*, *Heliotropium*, *Tournefortia*.]

BACIU, V. A. Anatomia fructelor de Boraginee, cu accentuarea ontogenezei elaiosomului și a detașării mericarpiilor. (French summary.) *Bul. Facul. Științe Cern.* 9: 123-169. 1935. [Fruit anatomy, development of the elaiosomes, and detachment of nutlets in 16 genera; *Borago*, *Cynoglossum*, *Echium*, *Lithospermum*, *Myosotis*, *Symphytum*; a related paper in *Ibid.* 5: 48-63. 1931.]

BAILEY, L. H. Manual of cultivated plants. 1116 pp. New York. 1949. [Boraginaceae, 830-839.]

———, E. Z. BAILEY, & BAILEY HORTORIUM STAFF. *Hortus* third. xiv + 1290 pp. New York and London. 1976.

BAILLON, H. Boraginacées. *Hist. Pl.* 10: 343-402. 1890. [Including Hydrophyllaceae.]

BAKER, J. G., & C. H. WRIGHT. Boraginaceae. In: W. T. THISTELTON-DYER, ed., *Fl. Tropical Africa* 4(2): 5-62. 1906.

BALL, P. W. *Onosma*. In: T. G. TUTIN *et al.*, eds. *Fl. Europaea* 3: 89-94. 1972. [Thirty-three species.]

BANERJEE, S. P., & R. N. BANERJEE. A taxonomic revision of Indian *Microroula* Benth. (Boraginaceae). *Bull. Bot. Surv. India* 15: 71-75. 1973.

——— & A. BHATTACHARJEE. Notes on *Microcaryum* Johnst. and *Lasiocaryum* Johnst. (Boraginaceae) in India. *Bull. Bot. Soc. Bengal* 39: 33-39. 1985. [Genera of the tribe Eritrichieae endemic to the Himalayas and Central Asia.]

——— & B. B. PRAMANIK. A taxonomic revision of Indo-Burmese *Trichodesma* R. Br. (Boraginaceae). *Bull. Bot. Surv. India* 17: 108-123. 1975. [Seven species; key, descriptions, distributions.]

BARAJAS MORALES, J. Descriptions and notes on the wood anatomy of Boraginaceae from western Mexico. *IAWA Bull.* II. 2: 61-67. 1981. [*Bourreria*, *Cordia*; light microscopy, wood of six species, occurrence of starch grains, vested pits, and silica grains.]

———. Detalles ultraestructurales de la madera de algunas Boraginaceae de México. (English summary.) *Bol. Soc. Bot. Méx.* 45: 3-14. 1983. [A species of *Bourreria* and three of *Cordia*; occurrence of vested pits, calcium oxalate crystals, and tyloses, 24 scanning-electron microscope photographs.]

BAMBIER, E., & J. MATHEZ. Contribution à l'étude des Cynoglossées (Boraginacées): *Pardoglossum*, genre nouveau du Bassin méditerranéen occidental. (English summary.) *Candollea* 28: 281-323. 11 pls. 1973. [Morphology and palynology of *Caccinia*, *Cynoglossum*, *Kuschakeviczia*, *Lindelofia*, *Mattias-trum*, *Omphalodes*, *Paracaryum*, *Pardoglossum*, *Rindera*, *Solenanthus*, *Suchtelenia*, *Trichodesma*; nutlet morphology and anatomy of *Cynoglossum* and *Pardoglossum*.]

- BARRETT, S. C. H. The evolution, maintenance, and loss of self-incompatibility systems. Pp. 98-124 in J. L. DOUST & L. L. DOUST, eds., *Plant reproductive ecology: patterns and strategies*. New York and Oxford. 1988. [Boraginaceae, 103, 104.]
- BATES, V. The vascular plants of Tennessee: a taxonomic and geographic guide to the floristic literature. *Jour. Tenn. Acad. Sci.* **60**: 66-76. 1985.
- BATE-SMITH, E. C. The phenolic constituents of plants and their taxonomic significance. *Jour. Linn. Soc. Bot.* **58**: 95-173. 1962. [Boraginaceae, 155; flavonoids of 11 species, including three of *Cordia* and one each of *Anchusa*, *Echium*, *Lindlofia*, *Lithospermum*, *Macrotomia*, *Mertensia*, *Pulmonaria*, *Symphytum*.]
- BAYER DE KRAEMER, G.-I. Karpologische Untersuchungen an Boraginaceae. *Dipl. Arb. München*. 1970.*
- BEHNKE, H.-D., & W. BARTHOLOTT. New evidence from the ultrastructural and micromorphological fields in angiosperm classification. *Nordic Jour. Bot.* **3**: 43-66. 1983. [Boraginaceae, 48, 52, 62; crystalline inclusions of the sieve-element nuclei.]
- BELL, C. R., & B. J. TAYLOR. Florida wild flowers and roadside plants. *Frontisp.* + xxi + 308 pp. Chapel Hill, North Carolina. 1982. [Color photographs and brief descriptions of *Cordia Sebestena*, *Heliotropium angiospermum*, *Lithospermum carolinense*, *Tournefortia gnaphalodes*.]
- BELVAL, H., & L. EVIN. Sur la présence de fructosanes dans les Boraginées. *Compt. Rend. Acad. Sci. Paris* **216**: 900-902. 1943. [Occurrence in *Symphytum officinale*.]
- BEN SAAD-LIMAN, S., & M. A. NABLI. Ultrastructure de l'exine de l'*Arnebia decumbens* (Vent.) Coss. et Kral. et du *Cerinthe major* L. (Boraginaceae). (English summary.) *Pollen et Spores* **24**: 9-19. 1982.
- BENSON, L. Plant classification. ed. 2. *Frontisp.* + xxiv + 901 pp. Lexington, Massachusetts and Toronto. 1979. [Boraginaceae, 270, 274, 276, 508, 509.]
- BENTHAM, G., & J. D. HOOKER. Boragineae. *Gen. Pl.* **2**: 832-865. 1876. [Tribes Cordieae, Ehretiaeae, Heliotropieae, and Borageae; 68 genera recognized; family placed between Hydrophyllaceae and Convolvulaceae; treatment by BENTHAM.]
- BERMAN, A. Recherches sur la structure anatomique du fruit des Boraginacées. Thesis, Facul. Pharm. Paris. 1926.*
- BESSEY, C. E. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* **2**: 109-164. 1915. [Boraginaceae, 145; placed in the order Polemoniales, including also the Polemoniaceae, Convolvulaceae, Hydrophyllaceae, Nolanaceae, and Solanaceae.]
- BHATTACHARYA, G. N. Chromosome studies in Boraginaceae. *Bull. Bot. Soc. Bengal* **22**: 79-82. 1968. [*Cordia Aubletii*, *C. Sebestena*, *Ehretia acuminata*, *Heliotropium indicum*; karyotypes.]
- BIDER, J. Beiträge zur Pharmakognosie der Boraginaceen und Verbenaceen. Vergleichende Anatomie des Laubblattes. Thesis, 124 pp., Basel. 1935.*
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. In: A. A. FEDOROV, ed., *Chromosome numbers of flowering plants*. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Boraginaceae, 156-162.]
- BOLLIGER, M. Die Gattung *Pulmonaria* in Westeuropa. (English and French summaries.) *Phanerogam. Monogr.* **8**. 215 pp. Vaduz. 1982. [Morphology, karyology, geography, ecology.]
- BOURDU, R. Contribution à l'étude du métabolisme glucidique des boraginacées. *Rev. Gén. Bot.* **64**: 152-192. 1957. [*Pulmonaria longifolia*, *Symphytum officinale*; chromatographic analysis of sugar content of various organs.]
- BRAMWELL, D. Boraginaceae. Pp. 235, 236 in V. H. HEYWOOD *et al.*, eds., *Flowering plants of the world*. 335 pp. New York. 1978.
- BRAND, A. Neue Gattungen und Arten der Cynoglosseae. *Repert. Sp. Nov. Reg. Veg.* **13**: 545-550. 1915a. [Including *Adelocaryum* and *Bilegnum*, new genera.]

- . Neue Boraginaceen-Studien. *Ibid.* 14: 146–156. 1915b. [New taxa of *Lappula*; *Mattiastrum*, gen. nov.]
- . Boraginaceae-Boraginoideae-Cynoglosseae. In: A. ENGLER, Pflanzenr. IV. 252 (Heft 78): 1–183. 1921. [Detailed study on worldwide basis of 20 genera.]
- . Drei neue Gattungen der Cryptanthaeae. *Repert. Sp. Nov. Reg. Veg.* 21: 249–254. 1925. [*Echinoglochin*, *Johnstonella*, *Pedinogyne*.]
- . Boraginaceae-Boraginoideae-Cryptanthaeae. In: A. ENGLER, ed., Pflanzenr. IV. 252 (Heft 97): 1–236. 1931. [Comprehensive account of 33 genera, including *Amsinckia*, *Hackelia*, *Lappula*, *Plagiobothrys*.]
- BREEMEN, A. M. M. VAN. Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* 33: 283–305. 1984. [*Anchusa carvensis*, *Cynoglossum officinale*, *Echium vulgare*.]
- BRESINSKY, A. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. (English summary.) *Bibliot. Bot.* 126. 54 pp. 1963. [Anatomy, chemical constituents, and dispersal importance of elaiosomes in numerous species of various families; Boraginaceae, 21, 22; genera studied include *Anchusa*, *Pulmonaria*, and *Symphytum*.]
- BREWBAKER, J. L. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. *Am. Jour. Bot.* 54: 1069–1083. 1967. [Boraginaceae, 1076, 1077; binucleate pollen in three genera and trinucleate pollen in 16 others.]
- BRIECHLE, M., & H. H. HILGER. Die Embryogenese von *Microparacaryum intermedium* und die embryogenetische Klassifizierung der Boraginaceae. (English summary.) *Flora* 181: 45–59. 1988. [Embryogeny of *Microparacaryum* resembles that of *Hyoscyamus*; review of embryogenic types in the Boraginaceae.]
- BRITTON, D. M. Cytogenetic studies on the Boraginaceae. *Brittonia* 7: 233–266. 1951. [A comprehensive cytological account of the Boraginaceae to 1950.]
- BROWICZ, K. The genus *Lithodora* Griseb. (Boraginaceae) in the eastern Mediterranean region. *Ann. Mus. Goulandris* 7: 39–48. 1986.
- BRUMMITT, R. K. *Ogastemma*, a new name for *Megastoma* (Boraginaceae). *Kew Bull.* 36: 679, 680. 1982a. [The monotypic *Megastoma* when validated became a later homonym for a genus of algae.]
- . A revision of *Trichodesma* sect. *Friedrichsthalia* (Fenzl) A. DC. non Brand (Boraginaceae). *Kew Bull.* 37: 429–450. 1982b. [Sectional evaluation, five species recognized in Tropical Africa.]
- . Notes on some African and Arabian species of *Trichodesma* (Boraginaceae). *Kew Bull.* 40: 851–854. 1985.
- BULL, L. B., C. C. J. CULVENOR, & A. T. DICK. The pyrrolizidine alkaloids. Their occurrence, pathogenicity and other biological properties. In: A. NEUBERGER & E. L. TATUM, eds., *Frontiers of biology*. Vol. 9. xv + 293 pp. New York. 1968. [Poisoning by *Amsinckia*, *Echium*, *Heliotropium*, *Trichodesma*; types of alkaloids and their distribution; toxicity, chemical, physical and biological properties, pathogenicity; Boraginaceae, 234–238; excellent literature survey.]
- BURKILL, H. M. The useful plants of West Tropical Africa. ed. 2. Vol. 1 (Families A–D). *Frontisp.* + xvi + 960 pp. Kew. 1985. [Boraginaceae, 285–297; *Coldenia*, *Cordia*, *Cynoglossum*, *Echium*, *Ehretia*, *Heliotropium*, *Moltkia*, *Trichodesma*.]
- BURKILL, I. H. A dictionary of the economic products of the Malay Peninsula. 2 vols. London. 1935. [*Cordia*, *Heliotropium*, *Symphytum*, *Tournefortia*.]
- CANDOLLE, A. P. DE. Boragineae. *Prodr.* 9: 466–559. 1845; 10: 1–177, 587, 588. 1846. [Family divided into tribes Cordieae, Ehretieae, Heliotropieae (treated in vol. 9) and Borageae (vol. 10); the last divided into six subtribes.]
- CANTINO, P. D. Affinities of the Lamiales: a cladistic analysis. *Syst. Bot.* 7: 237–248. 1982. [The Lamiales united with the Scrophulariales by more synapomorphies than with the Boraginaceae.]

- CARLQUIST, S. Comparative wood anatomy. x + 436 pp. Berlin and other cities. 1988.
- CASPER, B. B. Self-compatibility in distylous *Cryptantha flava* (Boraginaceae). New Phytol. 99: 149-154. 1985. [Lack of inhibition of pollen-tube growth following selfing or intramorph pollination.]
- & T. R. LA PINE. Changes in corolla color and other floral characteristics in *Cryptantha humilis* (Boraginaceae): cues to discourage pollinators? Evolution 38: 128-141. 1984.
- & D. WIENS. Fixed rates of random ovule abortion in *Cryptantha flava* (Boraginaceae) and its possible relation to seed dispersal. Ecology 62: 866-869. 1981. [Wind dispersal of persistent nutlets by fruiting calyces.]
- CHANT, S. R. Ehretiaceae. Pp. 233, 234 in V. H. HEYWOOD *et al.*, eds., Flowering plants of the world. 335 pp. New York. 1978.
- CHAPMAN, A. W. Flora of the southern United States. ed. 3. xxix + 655 pp. Cambridge, Massachusetts. 1897. [Boraginaceae, 357-363.]
- CHATER, A. O. The nomenclature of the European species of *Elizaldia* Willk. (Boraginaceae). Bot. Jour. Linn. Soc. 64: 67-69. 1971. [Two subspecies of *E. calycina*.]
- CHUKAVINA, A. P. A new genus of Boraginaceae. Dokl. Akad. Nauk. Tadzh. SSR 17(9): 63-66. 1974.* [*Scapicephalus rosulatus*, gen. et sp. nov.]
- CLARKE, C. B. Boraginaceae. In: J. D. HOOKER, Fl. British India 4: 134-179. 1885.
- CLARKE, G. C. S. The northwest European pollen flora, 10. Boraginaceae. Rev. Palaeobot. Palynol. 24: 59-101. 1977. [*Amsinckia*, *Anchusa*, *Borago*, *Buglossoides*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lappula*, *Lithospermum*, *Mertensia*, *Myosotis*, *Nonea*, *Pentaglottis*, *Pulmonaria*, *Symphytum*, *Trachystemon*.]
- , S. CHANDA, & S. SAHAY. Pollen morphology in the genus *Pardoglossum* (Boraginaceae) with some observations on heterocolpate pollen. *Ibid.* 28: 301-309. 1979. [Five species with heterocolpate pollen, comparison with some members of the Cynoglosseae.]
- CLEWELL, A. F. Guide to the vascular plants of the Florida panhandle. viii + 605 pp. Tallahassee, Florida. 1985. [Boraginaceae, 255-257; *Buglossoides*, *Cynoglossum*, *Heliotropium*, *Lithospermum*, *Myosotis*, *Onosmodium*.]
- CLUTE, W. N. The meaning of plant names. XXX. The borageworts. Am. Bot. 33: 55-60. 1927. [Origin of common names of several naturalized species of Boraginaceae; a related paper in *ibid.* 32: 148-151. 1926.]
- COCHRANE, T. S. Notes on the flora of Wisconsin - I. New and corrected distribution records of Boraginaceae. Michigan Bot. 14: 115-123. 1975.
- COCKERELL, T. D. A. The name of a fossil boraginaceous plant. Torreyia 33: 15. 1933. [Nutlets from the Upper Tertiary assigned to *Biorbia*.]
- COCUCCI, A. E. New evidence from embryology in angiosperm classification. Nordic Jour. Bot. 3: 67-73. 1983. [Realignment of the Boraginaceae, 67, 68; see DI FULVIO (1979).]
- CORNER, E. J. H. The seeds of dicotyledons. Vol. 1 (text), ix + 311 pp., vol. 2 (illustrations), vi + 552 pp. 1976. [Boraginaceae, 1: 82, 83.]
- CORRELL, D. S., & H. B. CORRELL. Aquatic and wetland plants of southwestern United States. xv + 1777 pp. Washington, D.C. 1972. (Reprinted in 2 vols., Stanford. 1975.) [Boraginaceae, 1383-1392; *Hackelia*, *Heliotropium*, *Mertensia*, *Myosotis*.]
- & ———. Flora of the Bahama Archipelago. *Frontisp.* + 50 + 1692 pp. Vaduz. 1982. [Boraginaceae, 1193-1215; *Bourreria*, *Cordia*, *Heliotropium*, *Mallotonia*, *Rochefortia*, *Tournefortia*.]
- & M. C. JOHNSTON. Manual of the vascular plants of Texas. *Frontisp.* + xv + colored map + 1881 pp. Renner, Texas. 1970. [Boraginaceae, 1280-1311, 1739, 1740.]

- CRÉTÉ, P. Embryogénie des Boragacées. Développement de l'embryon chez *Anchusa officinalis* L. Compt. Rend. Acad. Sci. Paris **230**: 1198, 1999. 1950.
- . Embryogénie des Boragacées. Développement de l'embryon chez l'*Alkanna lutea* A. DC. (*Nonnea lutea* DC.). *Ibid.* **232**: 1689–1691. 1951.
- . Embryogénie des Boragacées. Développement de l'embryon chez l'*Eritrichium strictum* Decne. *Ibid.* **236**: 224–226. 1953.
- . Embryogénie des Boragacées. Développement du proembryon chez le *Pulmonaria officinalis* L. *Ibid.* **249**: 2095–2097. 1959.
- CRONQUIST, A. Boraginaceae. In: C. L. HITCHCOCK, A. CRONQUIST, & M. OWNBEY. Vasc. Pl. Pacific Northwest **4**: 175–244. 1959.
- . An integrated system of classification of flowering plants. *Frontisp.* + xviii + 1262 pp. New York. 1981. [Lamiales, 910–927; Boraginaceae, 917–920.]
- . Boraginaceae. In: A. CRONQUIST, A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, & P. K. HOLMGREN. Intermountain Fl. **4**: 207–293. 1984.
- . The evolution and classification of flowering plants. ed. 2. *Frontisp.* + viii + 555 pp. Bronx, New York. 1988. [Boraginaceae, 428; family placed with the Lamiaceae, Lennoaceae, and Verbenaceae in the Lamiales.]
- CULVENOR, C. C. J. Tumor-inhibitory activity of pyrrolizidine alkaloids. Jour. Pharm. Sci. **57**: 1112–1117. 1968. [Alkaloids of the Boraginaceae and other families.]
- . Pyrrolizidine alkaloids—occurrence and systematic importance in angiosperms. Bot. Not. **131**: 473–486. 1978. [Structure, biosynthesis, and distribution of pyrrolizidine alkaloids; occurrence in the Boraginaceae; compounds not useful taxonomically above the family level.]
- DAHLGREN, K. V. O. Vererbung der Heterostylie bei *Fagopyrum* (nebst einigen Notizen über *Pulmonaria*). (English summary.) Hereditas **3**: 91–99. 1922. [*P. officinalis*; selfing of long-styled form produced few nutlets, but selfing of short-styled ones produced many fruits.]
- DAHLGREN, R. M. T. A note on the taxonomy of the "Sympetalae" and related groups. Publ. Cairo Univ. Herb. **7/8**: 83–102. 1977. [Boraginaceae, 88, 92; segregates of Boraginaceae recognized, all placed in Boraginales along with Solanales in one superorder.]
- . A revised system of classification of the angiosperms. Bot. Jour. Linn. Soc. **80**: 91–124. 1980. [Boraginales and Solanales placed in superorder Solaniflorae, 104.]
- . General aspects of angiosperm evolution and macrosystematics. Nordic Jour. Bot. **3**: 119–149. 1983. [Boraginales, 138, 144; placed in the superorder Solaniflorae.]
- , S. ROSENDAL-JENSEN, & B. J. NIELSEN. A revised classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149–204 in D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. New York. 1981. [Boraginales, 202.]
- D'AMATO, G., & Z. TROJANI. Giemsa banding and karyotype in three species of *Anchusa* (Boraginaceae). Caryologia **38**: 13–22. 1985.
- DARWIN, C. The different forms of flowers on plants of the same species. viii + 352 pp. New York. 1877. [*Cordia*, 117, 118, 253; *Pulmonaria* spp., 101–111.]
- DAVIS, G. L. Systematic embryology of the angiosperms. viii + 528 pp. New York, London, and Sydney. 1966. [Boraginaceae, 60, 61.]
- DAVIS, P. H., ed. Boraginaceae. Fl. Turkey **6**: 237–437. 1978. [Thirty-three genera. See also supplement, Fl. Turkey **10**: 182–191, 249, 260, 261, 320, 321, 460, 461, 489, 493, 497, 499, 510. 1988.]
- DEAM, C. C. Flora of Indiana. 1236 pp. Indianapolis. 1940. [Boraginaceae, 787–795, 1082, 1083.]
- DEAN, B. E., A. MASON, & J. L. THOMAS. Wildflowers of Alabama and adjoining states. xxii + 230. [Tuscaloosa,] Alabama. 1973. [Colored photographs

and notes on *Echium vulgare*, *Heliotropium indicum*, *Lithospermum canescens*, *Mertensia virginica*.]

- DÍEZ, M. J. Pollen-morphology of genus *Anchusa* L. (Boraginaceae). Its taxonomic interest. Pollen et Spores **25**: 367-381. 1983. [Pollen supports the subgeneric classification of *Anchusa*.]
- . Contribución al atlas palinológico de Andalucía Occidental, I. Boraginaceae. (English summary.) Lagascalia **13**: 147-171. 4 pls. 1984. [Light and scanning-electron microscopy of pollen of 43 taxa in *Alkanna*, *Anchusa*, *Borago*, *Cerinthe*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lithodora*, *Myosotis*, *Neotostema*, *Nonea*; key to genera based on pollen morphology; taxonomic importance.]
- DI FULVIO, T. E. Sobre la embriología de *Cortesia cuneifolia* (Boraginaceae). I. Anatomía floral, esporogénesis y gametogénesis. (English summary.) Kurtzi-ana **2**: 7-25. 1965a. [Embryological data support the placement of *Cortesia* in the Ehretioideae.]
- . Recuentos cromosómicos en Boraginaceae. *Ibid.* **2**: 131-133. 1965b. [*Amisackia*, *Echium*, *Plagiobothrys*.]
- . Cromosomas gaméticos de *Patagonula americana* L. (Boraginaceae). *Ibid.* **5**: 402. 1969. [*n* = 18.]
- . Sobre la vasculatura floral, embriología y cromosomas de *Izorhea tschudiana* (Heliotropiaceae). (English summary.) *Ibid.* **11**: 75-105. 1978. [Floral anatomy, mega- and micro-sporogenesis, fertilization, embryogeny, fruit development; position of genus; relationship of Heliotropioideae to Ehretioideae.]
- . El endosperma y el embrión en el sistema de Tubiflorae, con especial referencia a Boraginaceae y Hydrophyllaceae. (English summary.) *Ibid.* **12/13**: 101-112. 1979. [Embryological data support the separation of Cordioideae, Ehretioideae, and Heliotropioideae in one family (Heliotropiaceae) placed in a different order from the remainder of the Boraginaceae.]
- . Sobre el polen de *Izorhea tschudiana* (Heliotropiaceae). (English summary.) Bol. Soc. Argent. Bot. **19**: 83-90. 1980. [Pollen morphology and germination; pollen 3-zonocolporate, oblate-spheroidal, with 3-pseudocolpi.]
- DOBROCHAEVA, D. M. Quantitative composition and analysis of Boraginaceae Lindl. flora (Boraginales Hutch.) in the European section of the USSR. (In Russian; English summary.) Ukrain. Bot. Zhur. **34**: 604-611. 1977. [Thirty genera and 143 species, the Heliotropiaceae maintained.]
- DUKE, J. A. On tropical tree seedlings. I. Seeds, seedlings, systems, and systematics. Ann. Missouri Bot. Gard. **56**: 125-161. 1969. [Cordiaceae, 158.]
- & E. S. AYENSU. Medicinal plants of China. 2 vols. 705 pp. Algonac, Michigan. 1985. [Boraginaceae, 202-206; *Arnebia*, *Cynoglossum*, *Heliotropium*, *Lithospermum*, *Onosma*, *Trigonotis*.]
- DULBERGER, R. Floral dimorphism in *Anchusa hybrida* Ten. Israel Jour. Bot. **19**: 37-41. 1970. [*Anchusa undulata*, heterostyly.]
- DUNCAN, W. H., & L. E. FOOTE. Wildflowers of the southeastern United States. vii + 296 pp. Athens, Georgia. 1975. [Boraginaceae, 148, 149; *Heliotropium*, *Lithospermum*, *Mertensia*.]
- & J. T. KARTESZ. Vascular flora of Georgia. An annotated checklist. ix + 143 + 3 unnumbered index pp. Athens, Georgia. 1981. [Boraginaceae, 109, 110.]
- DYER, R. A. The genera of southern African flowering plants. Vol. 1. Dicotyledons. map + 756 pp. Pretoria. 1975. [Boraginaceae, 508-514.]
- EDGAR, J. A., & C. C. J. CULVENOR. Pyrrolizidine ester alkaloids in danaid butterflies. Nature **248**: 614-616. 1974. [Male butterflies of the subfamily Danainae feed on pyrrolizidine-containing plants and utilize these compounds to produce sex pheromones.]
- , ——— & T. E. PLISKE. Coevolution of danaid butterflies with their host plants. *Ibid.* **250**: 646-648. 1974. [Pyrrolizidine alkaloids from Boraginaceae used by adults as sex attractants.]

- ELIAS, M. K. Tertiary grasses and other prairie vegetation from High Plains of North America. *Am. Jour. Sci.* **29**: 24–33. 1935. [*Krynitzkia Chaneyi*.]
- ELIAS, T. S. The complete trees of North America. Field guide and natural history. xii + 948 pp. New York and other cities. 1980. [Boraginaceae, 846–851; *Bourreria*, *Cordia*, *Ehretia*.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. *Frontisp.* + xii + 553 pp. New York. 1971. [Boraginaceae, 78–80.]
- EVERIST, S. L. Poisonous plants of Australia. xvi + 684 pp. Sydney. 1974. [Boraginaceae, 88–95; *Amsinckia*, *Buglossoides*, *Echium*, *Heliotropium*, *Symphytum*, *Trichodesma*.]
- FABRE, G. Les akènes des Boraginacées et leurs rapports avec l'habitat de la plante. *Bull. Soc. Bot. France* **113**(Mém. 1966): 212–216. 1967. [Fruit types of 53 species in 19 genera; habitats, illustrations.]
- & R. M. NICOLI. Sur la morphologie des akènes de quelques Boraginacées de la flore de France. Intérêt systématique de cette étude. *Ibid.* **121**: 133–144. 1974. [Fruit morphology and distinguishing features of numerous taxa; see FABRE.]
- FAVARGER, C. Recherches cytologiques sur quelques *Onosma* d'Europe occidentale. *Ann. Naturhist. Mus. Wien* **75**: 59–65. 1 pl. 1971.
- FEDOREEV, S. A., O. E. KRIVOSHCHKOVA, V. A. DENISENKO, P. G. GOROVoi, & O. B. MAKsimov. Quinoid pigments of Far Eastern representatives of the family Boraginaceae. *Chem. Nat. Compounds* **15**: 546–550. 1979. [*Cynoglossum*, *Echium*, *Eritrichium*, *Lappula*, *Lithospermum*, *Macrotomia*, *Mertensia*; occurrence of 11 pigments in roots of nine species.]
- FEINBRUN-DOTHAN, N. Boraginaceae. *Fl. Palaestina* **3**: 50–92. 1978. [Twenty-seven genera in three subfamilies and seven tribes.]
- FELL, K. R., & J. M. PECK. Phytochemical investigations of some species of the Boraginaceae. *Pl. Med.* **16**: 411–420. 1968. [*Borago officinalis*, *Symphytum* spp.; allantoin, alkaloids, sugars, amino acids.]
- FERNALD, M. L. Gray's manual of botany. ed. 8. lxiv + 1632 pp. New York and other cities. 1950. [Boraginaceae, 1195–1208.]
- FERNANDES, A., & M. T. LEITÃO. Contribution à la connaissance cytotaxonomique des Spermatophyta du Portugal. V. Boraginaceae. *Bol. Soc. Brot.* **46**: 389–405. 1972. [Chromosome numbers and karyotypes of 22 taxa, including species of *Borago*, *Buglossoides*, *Cynoglossum*, *Echium*, *Heliotropium*, *Symphytum*.]
- FOSTER, R. C. A catalogue of the ferns and flowering plants of Bolivia. *Contr. Gray Herb.* **184**: 1–223. 1958. [Boraginaceae, 166–168; 92 species in 12 genera.]
- FOURNET, J. Flore illustrée de phanérogames de Guadeloupe et Martinique. 1654 pp. Paris. 1978. [Boraginaceae, 1372–1390.]
- FRIES, R. E. Über den Bau der *Cortesia*-Blüte, ein Beitrag zur Morphologie und Systematik der Borragineen. *Ark. Bot.* **9**(13): 1–13. 1910.
- FÜRNKRANZ, D. Einige neue Boraginaceen-Chromosomenzahlen. (English summary.) *Österr. Bot. Zeitschr.* **114**: 341–345. 1967. [*Anchusa*, *Lithodora*, *Moltkia*, *Nonnea*.]
- GABEL, M. L. A fossil *Lithospermum* (Boraginaceae) from the Tertiary of South Dakota. *Am. Jour. Bot.* **74**: 1690–1693. 1987. [Nutlets of *Lithospermum*, review of fruit fossils of other genera.]
- GANDERS, F. R. The biology of heterostyly. *New Zealand Jour. Bot.* **17**: 607–635. 1979. [Boraginaceae, 610; a thorough review with excellent survey of the literature.]
- GATTINGER, A. The flora of Tennessee and a philosophy of botany. *Frontisp.* + 296 pp. Nashville, Tennessee. 1901. [Boraginaceae, 141–143.]
- GENTRY, J. L., JR. *Moritzia* DC. (Boraginaceae): a genus new to North America. *Fieldiana Bot.* **36**: 13–16. 1972. [The South American genus is reported from Costa Rica; key to the genera of Boraginaceae in Central America.]

- & D. JANOS. A preliminary generic key and geographic checklist of the Boraginaceae in Central America and Panama. *Phytologia* 27: 445–455. 1974.
- GERSHENZON, J., & T. J. MABRY. Secondary metabolites and the higher classification of angiosperms. *Nordic Jour. Bot.* 3: 5–34. 1983.
- GIBBS, R. D. Chemotaxonomy of flowering plants. 4 vols. 2372 pp. Montreal and London. 1974. [Boraginaceae, 1748–1751; tests for and occurrence of various compounds; vol. 4 includes bibliography, index, and addendum; many references to Boraginaceae.]
- GIBSON, D. N. Boraginaceae. In: P. C. STANDLEY & L. O. WILLIAMS, *Flora of Guatemala IX. Fieldiana Bot.* 24(9): 111–167. 1970.
- GLEASON, H. A. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 3. 589 pp. New York. 1952. [Boraginaceae, 109–125.]
- & A. CRONQUIST. Manual of vascular plants of northeastern United States and adjacent Canada. li + 810 pp. Princeton, Toronto, New York, and London. 1963. [Boraginaceae, 571–578.]
- GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetlands plants of southeastern United States. Dicotyledons. [x] + 933 pp. Athens, Georgia. 1981. [Boraginaceae, 580–585; *Heliotropium*, *Mertensia*, *Myosotis*.]
- GOLDBERG, A. Classification, evolution and phylogeny of the families of dicotyledons. *Smithson. Contr. Bot.* 58. iii + 314 pp. 1986. [Boraginaceae, 22, 23, 285; family placed in Polemoniales with Polemoniaceae, Fouquieriaceae, and Hydrophyllaceae.]
- GOLDBLATT, P., ed. Index to plant chromosome numbers, 1975–1978. *Monogr. Syst. Bot. Missouri Bot. Gard.* 5. vii + 554 pp. 1981. [Boraginaceae, 146–151.]
- , ed. Index to plant chromosome numbers, 1979–1981. *Ibid.* 8. viii + 427 pp. 1984. [Boraginaceae, 112–115.]
- , ed. Index to plant chromosome numbers, 1982–1983. *Ibid.* 13. [viii] + 224 pp. 1985. [Boraginaceae, 61–63.]
- , ed. Index to plant chromosome numbers, 1984–1985. *Ibid.* 23. [ix] + 264 pp. 1988. [Boraginaceae, 69–71.]
- & D. E. JOHNSON, eds. Index to plant chromosome numbers, 1986–1987. *Ibid.* 30. [vii] + 243 pp. 1990. [Boraginaceae, 56–58.]
- GOOD, R. Features of evolution in the flowering plants. x + 405 pp. New York. 1974. [Change in flower color of the Boraginaceae is associated with level of hydrogen-ion concentration, 326.]
- GOTTWALD, H. First description of the wood anatomy of *Antrophora*, *Lepidocordia* and *Pteleocarpa* (Boraginaceae). *IAWA Bull.* II. 3: 161–165. 1982. [*Pteleocarpa* has the most primitive wood in the family, wood anatomy strongly supports a close association between *Antrophora* and *Lepidocordia*.]
- GRAF, A. B. Tropica. Color cyclopedia of exotic plants and trees from the tropics and subtropics. 1120 pp. East Rutherford, New Jersey. 1978. [*Bourreria*, *Cordia*, *Echium*, *Heliotropium*, *Messerschmidia* (= *Argusia*), *Pulmonaria*, 196, 197, 955, 977, 993, 1011, 1066.]
- GRAHAM, A., & D. M. JARZEN. Studies in neotropical palaeobotany. I. The Oligocene communities of Puerto Rico. *Ann. Missouri Bot. Gard.* 56: 308–357. 1969. [*Tournefortia*, 316, 317, 330; see *Ibid.* 63: 787–842. 1976 for *Tournefortia* pollen from the Miocene of Veracruz, Mexico.]
- GRANT, V., & K. A. GRANT. A hummingbird-pollinated species of Boraginaceae in the Arizona flora. *Proc. Nat. Acad. Sci.* 66: 917–919. 1970. [Two species of hummingbirds pollinate *Macromeria viridiflora* var. *Thurberi*.]
- GRAU, J. Primäre und sekundäre Chromosomenbasiszahlen bei *Omphalodes*. *Österr. Bot. Zeitschr.* 114: 66–72. 1967. [Aneuploid change from the original base number of 12 to 11 or 14.]

- . Cytologische Untersuchungen an Boraginaceen I. Mitt. Bot. Staatssam. München 7: 277-294. 1968. [*Alkanna*, *Anchusa*, *Arnebia*, *Buglossoides*, *Eritrichum*, *Lithodora*, *Lithospermum*, *Moltkia*, *Omphalodes*, *Onosma*, *Symphytum*.]
- . Cytologische Untersuchungen an Boraginaceen II. (English summary.) *Ibid.* 9: 177-194. 1971. [*Elizaldia*, *Lithodora*, *Nonea*, *Onosma*, *Plagiobothrys*, *Symphytum*.]
- . Die annuellen Sippen von *Cryptantha* sect. *Cryptantha* in Chile. *Ibid.* 18: 379-400. 1982.
- . Life forms, reproductive biology and distribution of the Californian/Chilean genus *Cryptantha*. Dispersal and distribution. In: K. KUBITZKI, ed., Sonderabd. Naturwiss. Ver. Hamburg 7: 231-240. 1983. [Cleistogamy, dispersal, heterocarpy.]
- . Chromosomenzahlen chilenischer Boraginaceae. Mitt. Bot. Staatssam. München 27: 29-32. 1988. [Eight species; *Pectocarya*, *Plagiobothrys*.]
- GRAY, A. Synoptical flora of North America. Vol. 2. vi + 402 pp. New York. 1878. [Boraginaceae, 177-207.]
- . Contributions to the botany of North America. 1. A revision of some Borragineous genera. Proc. Am. Acad. Arts Sci. 20: 257-286. 1885. [A related paper in *ibid.* 10: 48-68. 1875.]
- GREENE, E. L. West American Asperifoliae.-IV. *Pittonia* 4: 86-97. 1899. [*Lappula*, *Lithospermum*, *Oreocarya*, *Mertensia*.]
- GREUTER, W. Med-checklist notulae, 3. *Willdenowia* 11: 23-43. 1981. [Boraginaceae, 32-39; *Mattiastrum*, *Paracaryum*, *Pardoglossum*, *Rindera*, and *Solenanthes* united with *Cynoglossum*; *Huynhia* and *Paramoltkia*, gen. nov.]
- GÜRKE, M. Boraginaceae. In: A. ENGLER & K. PRANTL, Nat. Pflanzenfam. IV. 3a: 71-131. 1897. [Eighty-five genera in four subfamilies, subfamily Boraginoideae divided into seven tribes.]
- GUNN, C. R., T. M. PULLEN, E. A. STADELBACHER, J. M. CHANDLER, & J. BARNES. Vascular flora of Washington County, Mississippi, and environs. vi + 150 pp. New Orleans. 1980. [*Hackelia*, *Heliotropium*, *Myosotis*; 58, 59.]
- GUPTA, H. P. Studies of Indian pollen grains-IV. Boraginaceae. *Geophytology* 1: 127-134. pl. 1971. [Thirty-one species in ten genera, including *Cordia*, *Cynoglossum*, *Heliotropium*, and *Mertensia*; relevance of pollen data in the intrafamilial classification of Boraginaceae.]
- GUŞULEAC, M. Zur Anatomie und Biologie der *Bothriospermum*- und *Thyrocarpus*-früchte. Beih. Bot. Centralbl. 43: 255-266. 1926. [Ovule and pericarp anatomy; tribal placement.]
- . Die europäischen Arten der Gattung *Anchusa* Linné. Bull. Facul. Stiinte 1: 73-123. 19 pls. 1927. [A related paper in *ibid.* 235-325. 5 pls.]
- . Species *Anchusae* generis Linn. hucusque cognitae. Repert. Sp. Nov. Reg. Veg. 26: 286-322. pls. 79-96. 1929. [Thirty-two species in six subgenera; plates republished from GUŞULEAC, 1927.]
- . Die monotypischen und artenarmen Gattungen der Anchuseae. *Ibid.* 29: 42-47, 113-125. pls. 109-114. 1931. [*Borago*, *Brunnera*, *Caryolopha*, *Gastrocotyle*, *Hormuzakia*, *Phyllocara*, *Procopiana*, *Trachystemon*. Paper published originally in Bull. Facul. Stiinte Cernăuţi 2: 394-461. 6 pls. 1928.]
- . Über die Orientierung des Ovulums bei den Boraginaceen und Labiaten, nebst Ausblicken auf das System dieser Familien. 28 pp. Cernăuţi. 1937.
- HALLIER, H. Provisional scheme of the natural (phylogenetic) system of flowering plants. New Phytol. 4: 151-162. 1905. [Boraginaceae, close to Verbenaceae, descendant of Bignoniaceae, and ancestral to Hydrophyllaceae, 162.]
- . L'origine et le système phylétique des angiospermes exposés à l'aide de leur arbre généalogique. Arch. Neerl. Sci. Exact. Nat. III. 1: 146-234 + 6 unnumbered pp. 1912. [Boraginaceae, 200, 201, 209.]

- HARRAR, E. S., & J. G. HARRAR. Guide to southern trees. ix + 712 pp. New York and London. 1941. [Boraginaceae, 639–644; *Bourreria*, *Cordia*.]
- HARTWELL, J. L. Plants used against cancer. A survey. *Lloydia* 31: 71–170. 1968. [Boraginaceae, 78–85.]
- HARVILL, A. M., JR., T. R. BRADLEY, & C. E. STEVENS. Atlas of the Virginia flora. Part 2. Dicotyledons. v + 61–148. Farmville, Virginia. 1981. [Boraginaceae, 82, 83.]
- HEDRICK, U. P., ed. Sturtevant's notes on edible plants. *Frontisp.* + vii + 686 pp. Albany, New York. 1919. [*Borago*, *Bourreria*, *Cordia*, *Symphytum*.]
- HEGI, G. Illustrierte Flora von Mittel-Europa. Vol. 5. part 3. München. 1927. [Boraginaceae, 2122–2232, pls. 219–222.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 3. Dicotyledonae: Acanthaceae–Cyrillaceae. 743 pp. Basel and Stuttgart. 1964. [Boraginaceae, 288–306, 646, 647; 8: 150–161, 702, 703. 1989.]
- . Cyanogenic compounds as systematic markers in Tracheophyta. *Pl. Syst. Evol. Suppl.* 1. 191–210. 1977. [Boraginaceae, 206, 208, 210.]
- HEINE, H. Boraginaceae. In: J. HUTCHINSON, J. M. DALZIEL, & F. N. HEPPER, eds., *Fl. West Trop. Africa*. ed. 2. 2: 317–325. 1963.
- HELSOP-HARRISON, Y., & K. R. SHIVANNA. The receptive surface of the angiosperm stigma. *Ann. Bot.* II. 41: 1233–1258. 4 pls. 1977. [Boraginaceae, 1239, 1242, 1245, 1251, 1253.]
- HIGGINS, L. C. A revision of *Cryptantha* subgenus *Oreocarya*. Brigham Young Univ. Sci. Bull. Biol. 13(4): iv + 63 pp. 1971. [Fifty-seven species; generic relationships, phylogeny, distribution, ecology; keys, maps, descriptions, distributions; see PAYSON.]
- . The Boraginaceae of Utah. *Ibid.* 16(3): 1–83. 1972. [Ninety-three species in 17 genera; keys, descriptions, distributions, maps.]
- . Boraginaceae of the southwestern United States. *Great Basin Nat.* 39: 293–350. 1979. [Eighteen genera and 113 species; area includes New Mexico, Arizona, southern Nevada, and southeastern California; keys, descriptions, references under individual genera.]
- & B. L. TURNER. *Antiphytum Hintoniorum* (Boraginaceae), a bizarre new gypsophile from North-Central Mexico. *Southwest Nat.* 28: 457, 458. 1983. [Brief account of the limits and distribution of *Antiphytum*.]
- HILGER, H. H. Die Perikarpentwicklung geflügelter Klausen aus dem *Paracaryum*-Verwandschaftskreis (Cynoglosseae, Boraginaceae). (English summary.) *Pl. Syst. Evol.* 138: 73–88. 1981a. [*Cynoglossum*, *Mattiastrum*, *Paracaryum*, *Rindera*; anatomy and development of nutlets; scanning-electron microscope photographs.]
- . Entwicklungstendenzen im Fruchtbau der anemochoren Boraginaceengattungen *Mattiastrum* und *Paracaryum*. (English summary.) *Ber. Deutsch. Bot. Ges.* 94: 677–687. 1981b. [Development and anatomy of the mericarp wing in 13 species of *Mattiastrum*, six of *Paracaryum*, and one of *Cynoglossum*.]
- . Wachstum und Ausbildungsformen des Gynoeceums von *Rochelia* (Boraginaceae). (English summary.) *Pl. Syst. Evol.* 146: 123–139. 1984. [Development of gynoecium and fruits, trends in reduction of nutlets, infrageneric classification; scanning-electron microscope photographs.]
- . Ontogenie, Morphologie und systematische Bedeutung geflügelter und glochidientragender Cynoglosseae- und Eritricheae-Früchte (Boraginaceae). (English summary.) *Bot. Jahrb.* 105: 323–378. 1985. [Development of flowers and fruits in 14 genera in three tribes, heterocarpy; scanning-electron microscope photographs.]
- . Mikromorphologische Untersuchungen an Klausenoberflächen von Boraginaceae. II. *Mattiastrum* (Boiss.) Brand (Cynoglosseae). (English summary.) *Beitr. Biol. Pflanzen* 61: 145–165. 1986. [Scanning-electron microscopy of nutlet surface of 29 species.]

- . Flower and fruit development in the Macaronesian endemic *Ceballosia fruticosa* (syn. *Messerschmidia fruticosa*, Boraginaceae, Heliotropioideae). *Pl. Syst. Evol.* **166**: 119–129. 1989. [Fruit morphology and anatomy, data support recognizing *Ceballosia* as distinct but closely related to *Heliotropium*.]
- , M. BALZER, W. FREY, & D. PODLECH. Heteromerikarpie und Fruchtpoly-morphismus bei *Microparacaryum*, gen. nov. (Boraginaceae). (English summary.) *Ibid.* **148**: 291–312. 1985. [Two species of *Microparacaryum* recognized, relationship to *Mattiastrum* and *Paracaryum* of the Cynoglosseae; variation in fruit morphology; nomenclatural adjustments.]
- HILL, A. F. Economic botany. ed. 2. xii + 560 pp. New York, Toronto, and London. 1952. [*Alkanna*, 131; *Heliotropium*, 187.]
- HOEFMANN, E., D. SCHLEE, & H. REINBOTHE. Zum Vorkommen und zur Verbreitung von Allantoin in Boraginaceen. (English summary.) *Flora (Abt. A, Physiol. Biochem.)* **159**: 510–518. 1969. [Survey of 74 species in 28 genera and three subfamilies.]
- HOMMERSAND, F. C. Boraginaceae. Pp. 878–887 in A. E. RADFORD, H. E. AHLES, & C. R. BELL, *Manual of the vascular flora of the Carolinas*. lxi + 1183 pp. 1968. [*Amsinckia*, *Cynoglossum*, *Echium*, *Hackelia*, *Heliotropium*, *Lithospermum*, *Mertensia*, *Myosotis*, *Onosmodium*, *Plagiobothrys*.]
- HOWARD, R. A. Boraginaceae. In: R. A. HOWARD, *Fl. Lesser Antilles* **6**: 188–211. 1989. [*Argusia*, *Bourreria*, *Cordia*, *Heliotropium*, *Rochefortia*, *Tournefortia*, *Trichodesma*.]
- HOWELL, J. T. The plant genus *Coldenia* in the Galapagos Islands. *Proc. Calif. Acad. Sci.* **22**: 99–110. pls. 26, 27. 1937. [Four endemic species.]
- HUIZING, H. J., & T. M. MALINGRÉ. A chemotaxonomical study of some Boraginaceae: pyrrolizidine alkaloids and phenolic compounds. *Pl. Syst. Evol.* **137**: 127–134. 1981. [Relevance of chemical data for the infrafamilial classification of the Boraginaceae.]
- HULTÉN, E. *Flora of Alaska and neighboring territories*. xxii + 1008 pp. Stanford, California. 1968. [Boraginaceae, 772–784.]
- HUNT, D. R. *Wellstedia* [spp.] Hooker's Icon. *Pl.* **37**: tt. 3665–3667. 1969. [Two species; descriptions, illustrations, distributions; excellent account of familial position of the genus, seven pages of text.]
- & J.-P. LEBRUN. A new *Wellstedia* from Ethiopia. *Kew Bull.* **30**: 222. 1975. [Genus includes three species: *W. filtuensis* (Ethiopia), *W. socotrana* (Socotra and Somalia), and *W. Dinteri* (South-West Africa and Cape Province).]
- HUNTER, C. G. *Wildflowers of Arkansas*. viii + 296 pp. Little Rock, Arkansas. 1984. [Boraginaceae, 180–183; color photographs and brief notes on *Cynoglossum virginicum*, *Echium vulgare*, *Heliotropium indicum*, *H. tenellum*, *Lithospermum canescens*, *Mertensia virginica*.]
- HUTCHINSON, J. *Evolution and phylogeny of flowering plants. Dicotyledons: facts and theory*. xxiv + 717 pp. London and New York. 1969. [Ehretiaceae, 465; Boraginaceae, 655–658.]
- . *The families of flowering plants*. ed. 3. xviii + 968 pp. Oxford. 1973. [Ehretiaceae in the Verbenales, 485, 486; Boraginaceae in the Boraginales, 622–624.]
- HUYNH, K.-L. Le pollen du genre *Arnebia* Forssk. et du genre *Macrotomia* DC. (Boraginaceae), et la position taxonomique particulière du *M. echioides* (L.) Boiss. (English summary.) *Candollea* **26**: 165–171. 1971.
- . Étude de l'arrangement du pollen dans la tétrade chez les angiospermes sur la base de données cytologiques. V. Le pollen hétéropolaire du genre *Onosma* (Boraginaceae). (English summary.) *Bull. Soc. Neuchâteloise Sci. Nat.* **95**: 5–10. 1972. [*O. helveticum*; arrangement of tricolporate pollen at tetrad stage.]

- IMBAMBA, S. K., & G. PAPA. Distribution of the kranz type anatomy in some dicotyledonous families of Kenya. *Photosynthetica* 13: 315-322. 1979. [Boraginaceae, 317, 318; 14 species of seven genera tested, only one of six species of *Heliotropium* has the "kranz type."]
- INGRAM, J. Studies in the cultivated Boraginaceae. 1. *Lithospermum* and related genera. *Baileya* 6: 90-100. 1958a. [*Buglossoides*, *Lithodora*, *Lithospermum*, *Moltkia*.]
- . Studies in the cultivated Boraginaceae. 2. *Echioides* and *Arnebia*. *Ibid.* 164-168. 1958b. [*A. decumbens*, *E. longiflorum*; key based on flower morphology to the genera *Arnebia*, *Echioides*, and *Lithospermum*.]
- . Studies in the cultivated Boraginaceae. 3. *Omphalodes*. *Ibid.* 8: 136-141. 1960. [Five species; key, notes, and illustrations.]
- . Studies in the cultivated Boraginaceae. 4. A key to the genera. *Ibid.* 9: 1-12, 56. 1961. [With illustrations of plants, flowers, and fruits of several genera.]
- ISHIKURA, N. Paper chromatographic survey of anthocyanins in four plants belonging to the family Boraginaceae. *Kumamoto Jour. Sci. Biol.* 12: 17-21. 1974. [*Cynoglossum amabile*, *Myosotis alpestris*, *Symphytum asperum*, and *Trigonotis peduncularis* contain delphinidin 3,5-diglucoside.]
- JAMIESON, G. R., & E. H. REID. The leaf lipids of some members of the Boraginaceae family. *Phytochemistry* 8: 1489-1494. 1969. [*Myosotis*, *Pulmonaria*, *Symphytum*; occurrence of 21 fatty acids in five species.]
- JODIN, H. Recherches anatomiques sur les Boraginées. *Ann. Sci. Nat. Bot.* VIII. 17: 263-272, 273-346. pls. 5-9. 1903. [Root, stem, petiole, and leaf blade anatomy, including species of *Amsinckia*, *Borago*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lithospermum*, *Myosotis*, and *Symphytum*; germination.]
- JOHANSEN, D. A. Plant embryology. xvi + 305 pp. Waltham, Massachusetts. 1950. [Boraginaceae, 220-222.]
- JOHNSTON, I. M. Studies in the Boraginaceae. *Contr. Gray Herb.* 68: 43-80. 1923. [Restoration of the genus *Hackelia*, 43-48. The genus *Antiphytum*, 48-52. Novelties and new combinations in the genus *Cryptantha*, 52-57. A synopsis and redefinition of the genus *Plagiobothrys*, 57-80.]
- . Studies in the Boraginaceae. — II. *Ibid.* 70: 1-61. 1924a. [A synopsis of the American native and immigrant borages of the subfamily Boraginoideae, 1-55; treatment of 31 genera, including *Amsinckia*, *Borago*, *Cynoglossum*, *Echium*, *Lithospermum*, *Lycopsis*, *Mertensia*, *Myosotis*, *Onosmodium*, *Symphytum*; tentative classification of the South American Coldenias, 55-61.]
- . Studies in the Boraginaceae. — III. *Ibid.* 73: 42-78. 1924b. [Critical evaluation of the tribal limits and generic lines of the Old World Boraginoideae; notes on 60 genera, including *Borago*, *Cynoglossum*, *Echium*, *Hackelia*, *Lithospermum*, *Mertensia*, *Myosotis*, *Plagiobothrys*, and *Symphytum*. New taxa and new combinations in miscellaneous American Boraginaceae.]
- . Studies in the Boraginaceae. — IV. The North American species of *Cryptantha*. *Ibid.* 74: 1-114. 1925a. [Generic limits and relationships, systematic position of the tribe Eritrichieae; treatment of 57 species, descriptions, distributions, key; subgenus *Oreocarya* recognized as a distinct genus; see HIGGINS (1971) and PAYSON.]
- . Studies in the Boraginaceae. — V. *Ibid.* 75: 40-49. 1925b. [Concerning the range and identity of certain American species, 40-44; notes on *Lithospermum*, *Myosotis*, and other genera. New or otherwise interesting Asiatic borages.]
- . Studies in the Boraginaceae. — VI. A revision of the South American Boraginoideae. *Ibid.* 78: 1-118. 1927. [Treatment of 17 genera, including *Amsinckia*, *Borago*, *Cynoglossum*, *Echium*, *Hackelia*, *Lappula*, *Lithospermum*, *Myosotis*, *Plagiobothrys*.]

- . Studies in the Boraginaceae. — VII. *Ibid.* 81: 3–83. 1928. [The South American species of *Heliotropium*, 3–73; treatment of 73 species in ten sections. Notes on various Boraginoideae, 73–83; five genera including *Plagiobothrys*.]
- . Studies in the Boraginaceae, IX. *Contr. Arnold Arb.* 3: 1–102. 1932. [The *Allocarya* section of *Plagiobothrys* in the western United States, 1–82. Notes on various borages of the western United States, 83–98; *Cryptantha*, *Heliotropium*, *Lappula*, *Mertensia*, *Pectocarya*.]
- . Studies in the Boraginaceae, X. The Boraginaceae of northeastern South America. *Jour. Arnold Arb.* 16: 1–64. 1935a. [*Cordia*, *Lepidocordia*, *Heliotropium*, *Tournefortia*; descriptions, distributions, keys; new taxa, notes on several species that also grow in the southeastern United States.].
- . Studies in the Boraginaceae, XI. *Ibid.* 145–205. 1935b. [The species of *Tournefortia* and *Messerschmidia* in the Old World, 145–168. Notes on BRAND's treatment of *Cryptantha*, 168–173. New or otherwise noteworthy species, 173–205; 16 genera, including *Amsinckia*, *Cordia*, *Hackelia*, *Heliotropium*, *Lithospermum*, *Plagiobothrys*, *Tournefortia*.]
- . Boraginaceae. In: A. PULLE, ed., *Fl. Suriname* 4: 306–333. 1936. [*Cordia*, *Heliotropium*, *Tournefortia*.]
- . Studies in the Boraginaceae, XII. *Jour. Arnold Arb.* 18: 1–25. 1937. [*Trigonotis* in southwestern China; new taxa and notes on several genera, including *Amsinckia*, *Cordia*, *Hackelia*, *Heliotropium*, *Lithospermum*, *Onosmodium*.]
- . Studies in the Boraginaceae, XIII. New or otherwise noteworthy species, chiefly from western United States. *Ibid.* 20: 375–402. 1939. [*Coldenia*, *Cryptantha*, *Hackelia*, *Heliotropium*, *Pectocarya*, *Plagiobothrys*.]
- . Studies in the Boraginaceae, XIV. Miscellaneous species from Asia, Malaysia and America. *Ibid.* 21: 48–66. 1940. [New taxa or new combinations in several genera, including *Bourreria*, *Hackelia*, *Heliotropium*.]
- . Studies in the Boraginaceae, XVI. Species chiefly from Mexico and western United States. *Ibid.* 29: 227–241. 1948. [New taxa in *Bourreria*, *Cordia*, *Cryptantha*, *Hackelia*, *Heliotropium*, and *Macromeria*; *Dasynotus*, gen. nov.].
- . Studies in the Boraginaceae, XVIII. Boraginaceae of the southern West Indies. *Ibid.* 30: 111–138. 1949. [*Bourreria*, *Cordia*, *Heliotropium*, *Rocheftoria*, *Tournefortia*.]
- . Studies in the Boraginaceae, XIX. *Ibid.* 31: 172–195. 1950. [*Antrophora*, gen. nov.; relationships to *Lepidocordia*; subfamilial relationships; *Cordia*.]
- . Studies in the Boraginaceae, XX. Representatives of three subfamilies in eastern Asia. *Ibid.* 32: 1–26, 99–122. 1951a. [*Carmona*, *Coldenia*, *Cordia*, *Ehretia*, *Heliotropium*, *Messerschmidia*, *Rotula*, *Tournefortia*.]
- . Studies in the Boraginaceae, XXI. Sino-Indian species of *Onosma*. *Ibid.* 201–255, 344–368. 1951b. [Thirty-eight species; descriptions, distributions, key.].
- . Studies in the Boraginaceae, XXII. Noteworthy species, chiefly Asian and South American. *Ibid.* 33: 62–78. 1952. [New taxa and new combinations in several genera, including South American *Cordia*.]
- . Studies in the Boraginaceae, XXIV. A. Three genera segregated from *Lithospermum*. B. Supplementary notes on *Lithospermum*. *Ibid.* 34: 1–16. 1953a. [*Mairetis*, *Moltkiopsis*, *Neatostema*, genera nov.].
- . Studies in the Boraginaceae, XXV. A revaluation of some genera of the Lithospermeae. *Ibid.* 258–299. 1953b. [*Alkanna*, *Echium*, *Halacsya*, *Lithodora*, *Lobostemon*, *Moltkia*.]
- . Studies in the Boraginaceae, XXVI. Further revaluations of the genera of the Lithospermeae. *Ibid.* 35: 1–81. 1954a. [Seventeen genera, including *Buglossoides*, *Lithospermum*, and *Onosmodium*.]
- . Studies in the Boraginaceae, XXVII. Some general observations concerning the Lithospermeae. *Ibid.* 158–166. 1954b. [Limits of the tribe Lithospermeae; key to its 23 genera.].

- . Studies in the Boraginaceae, XXVIII. New or otherwise interesting species from America and Asia. *Ibid.* **37**: 288–306. 1956. [*Bourreria*, *Coldenia*, *Cordia*, *Craniospermum*, *Hackelia*, *Heliotropium*, *Maharanga*, *Mertensia*, *Onosma*, *Tournefortia*.]
- . Studies in the Boraginaceae, XXIX. *Echiochilon* and related genera. *Ibid.* **38**: 255–293. 1957. [*Echiochilon*, *Megastoma*, *Sericostoma*.]
- . Some noteworthy American borages. *Wrightia* **2**: 13–22. 1959. [*Cryptantha*, *Heliotropium*, *Lasiarrhenum*, *Myosotis*.]
- , D. S. CORRELL, & F. C. HOMMERSAND. Boraginaceae. In: C. L. LUNDELL, *Fl. Texas* **1**: 123–221. 1966.
- JOHRI, B. M., & I. K. VASIL. The embryology of *Ehretia laevis* Roxb. *Phytomorphology* **6**: 134–143. 1956. [Brief review of embryology of the Boraginaceae.]
- JONES, S. B., JR., & N. C. COILE. The distribution of the vascular flora of Georgia. 230 pp. Athens, Georgia. 1988. [Boraginaceae, 75, 76; county distribution maps.]
- JONOVÁ, M. L'anatomie et la morphologie des trichomes des Boraginées à l'égard du système de cette famille. (In Czech; French summary.) *Zvlátní Vestn. Kral. Čes. Spol. Nauk.* **2**: 1–66. 1926.
- JOSHI, B. M. Studies in Boraginaceae: 1. Floral anatomy of *Bothriospermum tenellum* Fisch. et Mey. *Geobios Jodhpur* **2**: 10–12. 1975.*
- . Studies in Boraginaceae. Part 2. Morphology of gynoecium with special reference to evolution of the parietal placentation. *Ibid.* **3**(3): 76–78. 1976.*
- JUNELL, S. Über den Fruchtknotenbau der Boraginazeen mit pseudomonomeren Gynäzeen. *Sv. Bot. Tidskr.* **32**: 261–273. 1938.
- KAMINSKI, B. Flavonoids in the Boraginaceae family. Chromatographic investigation on glycoside fractions. *Acta Pol. Pharm. Trans.* **26**: 559–560. 1969.*
- II. Chromatographic investigation on aglycone fraction of bugloss (*Anchusa Gmelini* Led.) herb. *Ibid.* **28**: 89–92. 1971.*
- KAUL, R. B. Boraginaceae. Pp. 683–701 in T. M. BARKLEY, ed., *Flora of the Great Plains*. Lawrence, Kansas. 1986.
- KAZMI, S. M. A. A revision of the Boraginaceae of West Pakistan and Kashmir. *Jour. Arnold Arb.* **51**: 133–184, 367–402, 499–520. 1970; **52**: 110–136, 334–363, 486–522, 666–690. 1971. [Thirty-six genera; descriptions, keys, distributions.]
- . *Ivanjohnstonia jaunsariensis* — a new genus and species of Boraginaceae from North-West Himalayas. *Sultania* **1**: 1–4. 1975.
- KERNER VON MARILAUN, A. The natural history of plants. Their forms, growth, reproduction, and distribution. English translation by F. W. OLIVER. 4 half vols. [2 vols.] 777 + 983 pp. + 16 colored pls. New York. 1895. [*Borago*, *Cynoglossum*, *Echium*, *Lithospermum*, *Mertensia*, *Myosotis*.]
- KHALEEL, T. F. Embryology of *Trichodesma* (Boraginaceae). *Bot. Not.* **130**: 441–452. 1977a. [Two species; micro- and megasporogenesis, embryogeny; numerous illustrations.]
- . Embryology of *Ehretia acuminata* R. Br. *Proc. Montana Acad. Sci.* **37**: 35–53. 1977b. [Mega- and microsporogenesis, embryo development, pericarp and seed-coat anatomy.]
- KHANNA, P. Embryology of *Trichodesma amplexicaule* Roth. *Bull. Torrey Bot. Club* **91**: 105–114. 1964. [Including a brief discussion on embryological features of other Boraginaceae that differ from those of *Trichodesma*.]
- KIMPFLLIN, G. Sur les affinités des Boraginacées et des Lamiacées. *Ann. Soc. Linn. Lyon* **54**: 93–107. 1908. [Comparative morphology; stem anatomy and trichomes of a few selected genera.]
- KINGSBURY, J. M. Poisonous plants of the United States and Canada. xiii + 626 pp. Englewood Cliffs, New Jersey. 1964. [Boraginaceae, 271–275; *Amsinckia*, *Echium*, *Heliotropium*.]
- KLEIMAN, R., F. R. EARLE, I. A. WOLFF, & Q. JONES. Search for new industrial oils. XI. Oils of Boraginaceae. *Jour. Am. Oil Chem. Soc.* **41**: 459, 460.

1964. [Seed fatty acids of 29 species in 17 genera representing all tribes and subfamilies.]
- KLOTZ, G. Systematische Gliederung der Gattung *Rochefortia* Swartz. (English summary.) *Revista. Jard. Bot. Nac. Univ. Habana* 3(2): 99–110. 1982. [Twelve species in two sections and two series; genus primarily distributed in the West Indies, with outlying species in coastal northern South America and the Yucatán Peninsula, Mexico.]
- KNOBLOCH, I. W. Intergeneric hybridization in flowering plants. *Taxon* 21: 97–102. 1972. [Boraginaceae, 99; 47 hybrids known.]
- KNUTH, P. Handbuch der Blütenbiologie. Vol. 3, part 2. v + 601 pp. Leipzig. 1905. [Boraginaceae, 63–67.] English translation by J. R. A. DAVIS. Vol. 3. iv + 644 pp. Oxford. 1909. [Boraginaceae, 115–142; 23 genera, including *Borago*, *Cordia*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lithospermum*, *Lycopsis*, *Mertensia*, *Myosotis*, *Symphytum*.]
- KOUTNIK, D. L. Lectotypification in the genus *Lobostemon* (Boraginaceae). *Taxon* 34: 525–528. 1985. [Generic limits; lectotypification of eight species described by LEVYNS.]
- LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade, and Monroe counties, Florida. viii + 95 pp. Coral Gables, Florida. 1965. [*Bourreria*, *Cordia*, *Heliotropium*, *Tournefortia*; 76, 77.]
- LAWRENCE, G. H. M. Taxonomy of vascular plants. xiii + 823 pp. New York. 1951. [Boraginaceae, 684–686.]
- LAWRENCE, J. R. A correlation of the taxonomy and floral anatomy of certain of the Boraginaceae. *Am. Jour. Bot.* 24: 433–444. 1937. [Floral anatomy of representative genera of the various subfamilies and tribes of the family.]
- LECHNER-POCK, L. *Eritrichum nanum* (Amann) Schrader und seine Verwandten. *Phyton Austria* 6: 98–206. 1956. [Five species; detailed account of taxonomy on a worldwide basis.]
- LEVYNS, M. R. A revision of *Lobostemon* Lehm., and a discussion of the species problem. *Jour. Linn. Soc. Bot.* 49: 393–451. pl. 29. 1934. [Twenty-eight species in five sections; generic limits, species problems; *Echinostachys*, gen. nov.; see KOUTNIK.]
- LEWIS, W. H. Polyploidy in angiosperms: dicotyledons. Pp. 241–268 in W. H. LEWIS, ed., *Polyploidy: biological relevance*. New York and London. 1980. [Base chromosome number for the Boraginaceae may be 12, 254.]
- & M. P. F. ELVIN-LEWIS. Medical botany: plants affecting man's health. xv + 515 pp. New York and other cities. 1977. [Boraginaceae, 16, 55, 56, 93, 120, 133, 240, 342, 353, 389, 394; *Amsinckia*, *Borago*, *Cynoglossum*, *Echium*, *Ehretia*, *Heliotropium*, *Lithospermum*, *Tournefortia*, *Trichodesma*.]
- LITARDIÈRE, R. DE. Recherches caryologiques et caryo-taxonomiques sur les Boraginacées. *Bull. Soc. Hist. Nat. Afrique Nord* 32: 315–329. 1942.*
- LITTLE, E. L., JR. Atlas of United States trees. Vol. 5. Florida. U.S. Dep. Agr. Misc. Publ. 1361. vi + 22 pp. + 137 unnumbered pp. of maps and index. 1978. [*Bourreria*, *Cordia*, 12; maps 169, 170, 191.]
- . Checklist of United States trees (native and naturalized). U. S. Dep. Agr., Agr. Handb. 541. iv + 375 pp. 1979. [*Bourreria*, 64; *Cordia*, 96; *Ehretia*, 125.]
- LIU, Y.-L. Study on the genus *Onosma* L. of China. *Acta Phytotax. Sinica* 18: 63–70. pls. 7, 8. 1980. [Several new taxa.]
- LOEW, E. Ueber die Bestäubungseinrichtungen einiger Boragineen. *Ber. Deutsch. Bot. Ges.* 4: 152–178. pl. 8. 1886. [Floral adaptations to pollination, pollinators; *Anchusa*, *Arnebia*, *Borago*, *Caccinia*, *Echium*, *Symphytum*; notes on several species of other genera.]
- LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [*Bourreria*, *Cordia*, *Heliotropium*, *Tournefortia*; 726–732.]

- LOON, J. C. VAN. A cytotaxonomical atlas of the Balkan flora. In: A. & D. LÖVE, eds. Cytotaxonomical atlases. Vol. 4. Berlin and Stuttgart. 1987. [Boraginaceae, xvii, xviii, 156-165.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. 2 vols. New York. 1892. [Boraginaceae, 2: 253-266, 598.]
- LUQUE, T. Números cromosómicos de algunas Boragináceas de Portugal. (English summary.) Bol. Soc. Brot. II. 53: 663-670. 1980. [*Anchusa*, *Echium*, *Lithodora*.]
- . Estudio cariológico de Boragináceas Españolas, I. *Anchusa*. (English summary.) Lagasalia 12: 81-97. 4 pls. 1983. [Chromosome numbers and karyotypes of ten taxa; base chromosome number for *Anchusa* is eight.]
- MACBRIDE, J. F. Revision of the genus *Oreocarya*. Contr. Gray Herb. 48: 20-38. 1916. [A section of *Cryptantha*; see PAYSON.]
- . Boraginaceae. Fl. Peru. Publ. Field Mus. Nat. Hist. Bot. 13(5): 539-609. 1960.
- MACROBERTS, D. T. The vascular plants of Louisiana. An annotated checklist and bibliography of the vascular plants reported to grow without cultivation in Louisiana. Bull. Mus. Life Sci. Louisiana State Univ. Shreveport 6: 1-165. 1984. [Boraginaceae, 75, 76.]
- MALECKA, J. Cytological differentiation of the embryo sac in Boraginaceae. Acta Soc. Bot. Polon. 50: 147-150. 1981. [*Cerinthe major*, *Echium vulgare*, *Lithospermum arvense*, *Lycopsis arvensis*.]
- MANSFELD, R. Vorläufiges Verzeichnis landwirtschaftlich oder gärtnerisch kultivierter Pflanzenarten (mit Ausschluss von Zierpflanzen). Kulturpflanze Beih. 2: 1-659. 1959. [Boraginaceae 358-360; *Borago officinalis*, *Lithospermum officinale*, *Symphytum asperum*, *S. officinale*.]
- MARKOVA, M., & P. IVANOVA. Karyologische Untersuchung der Vertreter der Fam. Boraginaceae, Labiatae und Scrophulariaceae in Bulgarien. Mitt. Bot. Inst. Bulgaria 20: 93-97. 1970. [*Pulmonaria*, *Symphytum*.]
- & ———. Karyologische Untersuchung der Vertreter der Fam. Boraginaceae, Labiatae und Scrophulariaceae in Bulgarien. II. *Ibid.* 21: 123-131. 1971. [Karyotypes; *Anchusa italica*, *Cynoglossum hungaricum*, *Echium italicum*, *Echium vulgare*, *Heliotropium europaeum*, 123, 124.]
- MARTICORENA, C. Granos de polen de plantas chilenas. I. Gayana Bot. 17: 66 pp. 1968. [Boraginaceae, 37-58; *Amsinckia*, *Coldenia*, *Cordia*, *Cryptantha*, *Cynoglossum*, *Echium*, *Heliotropium*, *Myosotis*, *Nesocaryum*, *Pectocarya*, *Plagiobothrys*, *Selkirkia*.]
- MARTIN, A. C. Comparative internal morphology of seeds. Am. Midl. Nat. 36: 513-660. 1946. [Boraginaceae, 582, 608, 609.]
- MARTINS, E. S. New species of Boraginaceae from Flora Zambesiaca area. Garcia Orta Bot. 9: 71-77. 1987. [*Cordia*, *Cynoglossum*, *Cytostemon*, *Heliotropium*.]
- MATHUR, A. K., & U. B. MATHUR. Boraginaceae angiosperm seeds and their bearing on the age of Lameta beds of Gujarat, India. Curr. Sci. Bangalore 54: 1070, 1071. 1985.*
- MAURER, E. S. The scent of flowers and leaves; a search for fragrance among the minor natural orders. 4. The borage family (Boraginaceae). Manufact. Chem. 32(4): 176-178. 1961.*
- MEIKLE, R. D. Flora of Cyprus. Vol. 2. *Frontisp.* + xiii + 833-1969 + *map.* Kew. 1985. [Boraginaceae, 1119-1163.]
- MELCHIOR, H. A. Engler's Syllabus der Pflanzenfamilien, ed. 12. Vol. 2. 666 pp. Berlin. 1964. [Boraginaceae, 425, 431-434.]
- MERXMÜLLER, H., & J. GRAU. Dysplodie bei *Pulmonaria*. Rev. Roum. Biol. Bot. 14: 57-63. 1969.*
- METCALFE, C. R., & L. CHALK. Anatomy of the dicotyledons. 2 vols. lxiv + 1500 pp. Oxford. 1950. [Boraginaceae, 2: 945-954.]

- MIERS, J. On the comparative carpical structure of the Ehretiaceae and Cordiaceae. *Ann. Mag. Nat. Hist.* IV. 3: 383–388. 1869. [Cordiaceae maintained as a family distinct from the Boraginaceae, Ehretiaceae, and Heliotropiaceae.]
- MILL, R. R. Taxonomic studies on generic limits in the family Boraginaceae (Tribe Cynoglosseae). 861 pp. Unpubl. Ph.D. dissertation. Saint Andrews University, Scotland. 1979.
- . A revision of the genus *Afrotysonia* Rauschert (Boraginaceae). *Notes Bot. Gard. Edinburgh* 43: 467–475. 1986a. [Three species; affinities of the genus, palynology.]
- . A new name for *Adelocaryum erythraeum*. *Ibid.* 477–480. 1986b. [The new generic name *Brandella* proposed to accommodate *A. erythraeum*, after the transfer of all species originally described in *Adelocaryum* to other genera.]
- . A new *Solenanthus* (Boraginaceae) from China. *Ibid.* 44: 271–273. 1987. [Generic disposition and comparison of the new species with the genera *Craniospermum* and *Sinojohnstonia*.]
- . The taxonomic status of *Cynoglossum latifolium* (Boraginaceae). *Ibid.* 46: 43–47. 1989. [Species placed in the monotypic Australian genus *Austrocynoglossum*.]
- MILLER, A. G., & H. RIEDL. A revision of *Cystostemon* Balf. f. (Boraginaceae). *Notes Bot. Gard. Edinburgh* 40: 1–21. 1982. [*Vaupelia* is reduced to synonymy of *Cystostemon*; genus includes 13 species in two subgenera distributed in tropical Africa and southwestern Arabia.]
- MILLER, J. S. A revised treatment of Boraginaceae for Panama. *Ann. Missouri Bot. Gard.* 75: 456–521. 1988. [Fifty-two species in nine genera; floristic affinities, endemism, new taxa.]
- . A new combination in *Lepidocordia* (Boraginaceae). *Phytologia* 66: 476. 1989a. [*Antrophora* reduced to synonymy of *Lepidocordia*.]
- . A revision of the New World species of *Ehretia* (Boraginaceae). *Ann. Missouri Bot. Gard.* 76: 1050–1076. 1989b. [Generic limits and relationships within the Ehretioideae, key to genera; *Ehretia* includes three species in the New World; key to species, distribution, descriptions, variations.]
- MILLER, R. B. Vestured pits in Boraginaceae. *IAWA Bull.* 1977: 43–48. 1977. [Vestured pits found in *Echium*, *Pteleocarpa*, and *Rochefortia*; absent in 21 species of 8 other genera, including *Cordia*, *Heliotropium*, and *Tournefortia*; presence of these pits questionable in *Bourreria*.]
- MITCHELL, J., & A. ROOK. Botanical dermatology. xiii + 787 pp. Vancouver. 1979. [Boraginaceae, 140–142; *Borago*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lappula*, *Lycopsis*, *Myosotis*, *Pulmonaria*, *Symphytum*, *Tournefortia*.]
- MODILEVSKY, Y. S., & L. K. DZYUBENKO. Characteristics of heterostyly of *Pulmonaria officinalis* L. (In Ukrainian; English summary.) *Ukrain. Bot. Zhur.* 24(2): 15–23. 1967. [Megaspороgenesis; embryology following legitimate and illegitimate pollinations.]
- MOERMAN, D. E. Medicinal plants of native America. 2 vols. Univ. Michigan Mus. Anthropol. Tech. Rep. 19. 910 pp. 1986. [*Amsinckia*, 33; *Coldenia*, 128; *Cryptantha*, 141; *Cynoglossum*, 144; *Echium*, 159; *Hackelia*, 212; *Heliotropium*, 218, 219; *Lappula*, 159, 253; *Lithospermum*, 265, 266; *Mertensia*, 292; *Onosmodium*, 312; *Symphytum*, 473; Boraginaceae, 689, 690.]
- MOHR, C. Plant life of Alabama. xii + 921 pp. + 2 portraits + 13 pls. Montgomery, Alabama. 1901. (Reprinted from *Contr. U.S. Natl. Herb.* Vol. 6. 1901.) [Boraginaceae, 689–692.]
- MOORE, D. M. Flora Europaea check-list and chromosome index. x + 423 pp. Cambridge (England) and other cities. 1982. [Boraginaceae, 175–183.]
- MOORE, R. J., ed. Index to plant chromosome numbers. 1967–1971. *Regnum Veg.* 90. 539 pp. 1973. [Boraginaceae, 317–321.]
- , ed. Index to plant chromosome numbers for 1972. *Ibid.* 91. 108 pp. 1974. [Boraginaceae, 59–61.]

- , ed. Index to plant chromosome numbers for 1973/1974. *Ibid.* 96: 257 pp. 1977. [Boraginaceae, 30–33.]
- MORTON, J. F. Wild plants for survival in South Florida. ed. 4 (revised). 80 pp. Miami. 1977. [*Bourreria ovata*, 28; *Cordia Sebestena*, 38, 41.]
- MÜLLER, W. Beiträge zur Entwicklungsgeschichte der Infloreszenzen der Boragineen und Solaneen. *Flora* 94: 385–419. 1905. [*Heliotropium*, *Myosotis*, *Omphalodes*, *Symphytum*.]
- MUENSCHER, W. C. Weeds. ed. 2. xviii + 596 pp. Ithaca, New York. 1980. [Boraginaceae, 356–365; *Amsinckia*, *Cynoglossum*, *Echium*, *Hackelia*, *Heliotropium*, *Lappula*, *Lithospermum*, *Lycopsis*, *Symphytum*.]
- MULLER, J. Fossil pollen records of extant angiosperms. *Bot. Rev.* 47: 1–142. 1981. [Boraginaceae, 95, 96.]
- MUNZ, P. A. A California flora. *Frontisp.* + 1681 pp. Berkeley and Los Angeles. 1959. [Boraginaceae, 552–589.]
- NABIULLIN, A. A., S. A. FEDOREEV, & T. N. DESHKO. Circular dichroism of quinoid pigments from Far Eastern representatives of the family Boraginaceae. *Chem. Nat. Comp.* 19: 532–537. 1983.
- NAGARAJ, M., & T. FATHIMA. Embryological studies in *Rotula aquatica* Lour. *Proc. Indian Acad. Sci. B.* 66: 106–116. 1967. [Mega- and microsporogenesis, endosperm and embryo development.]
- & ———. A note on the sporogenesis and gametogenesis in *Adelocaryum*. *Curr. Sci. Bangalore* 37: 265–267. 1968. [*A. coelestinum*.]
- & ———. Studies on the structure and development of pericarp and seed coat in *Rotula aquatica* Lour. *Proc. Indian Acad. Sci. B.* 74: 314–318. 1971.
- NASH, D. L., & N. P. MORENO. Boraginaceae. *Fl. Veracruz* 18: 1–149. 1981. [*Borago*, *Cordia*, *Cynoglossum*, *Hackelia*, *Heliotropium*, *Lithospermum*, *Tournefortia*.]
- NESOM, G. L. Synopsis of the species of *Omphalodes* (Boraginaceae) native to the New World. *Sida* 13: 25–30. 1988. [Six Mexican species, one new.]
- . *Macromeria alba* (Boraginaceae), a new species from Tamaulipas, Mexico. *Madrôno* 36: 28–32. 1989.
- NETOLITZKY, F. Anatomie der Angiospermen-Samen. *Handb. Pflanzenanat.* II. Vol. 10. iv + 364 pp. 1926. [Boraginaceae, 276–277.]
- NEUBAUER, H. F. Über Knotenbau und Blattgrund von *Cordia Myxa* L., *Anchusa officinalis* L. und *Borago officinalis* L. (Boraginaceae). (English summary.) *Bot. Jahrb.* 98: 362–371. 1977. [Nodal anatomy; similarities among the three species.]
- NORTON, J. B. S. A coloring matter found in some Boraginaceae. *Rep. Missouri Bot. Gard.* 9: 149–151. 1898. [Occurrence of dyes in several North American plants, including species of *Lithospermum* and *Plagiobothrys*.]
- NOWICKE, J. W. Flora of Panama. Part IX. Family 167. Boraginaceae. *Ann. Missouri Bot. Gard.* 56: 33–69. 1969. [*Bourreria*, *Cordia*, *Cynoglossum*, *Ehretia*, *Hackelia*, *Heliotropium*, *Tournefortia*.]
- & J. S. MILLER. Pollen morphology of Cordioideae: *Auxemma*, *Cordia*, and *Patagonula*. (Abstr.) XIVth Int. Bot. Congr. Berlin. 292. 1987. [Pollen supports the sectional subdivisions of *Cordia*.]
- & ———. Pollen morphology and the relationships of Hoplestigmataceae. *Taxon* 38: 12–16. 1989. [Family retained in the Boraginales; pollen of *Bourreria* and *Ehretia*.]
- OH, S.-Y. A review of the family Boraginaceae of Korea. *Res. Rev. Kyungpook Natl. Univ.* 30: 329–370. 1980. [Twenty-nine taxa in 13 genera; synonymy, common names, habitats, distributions, maps.]
- OHWI, J. Flora of Japan (in English). Edited by F. G. MEYER & E. H. WALKER. *Frontisp.* + ix + 1067 pp. Smithsonian Inst., Washington, D.C. 1965. [Boraginaceae, 755–762.]

- OLESEN, J. M. Floral morphology and pollen flow in the heterostylous species *Pulmonaria obscura* Dumort. (Boraginaceae). New Phytol. **82**: 757-767. pl. 1979.
- ORNDUFF, R., ed. Index to plant chromosome numbers for 1965. Regnum Veg. **50**. viii + 128 pp. 1967. [Boraginaceae, 86.]
- . Index to plant chromosome numbers for 1966. *Ibid.* **55**. 126 pp. 1968. [Boraginaceae, 86.]
- . Index to plant chromosome numbers for 1967. *Ibid.* **59**. 126 pp. 1969. [Boraginaceae, 86, 87.]
- PAPAGEORGIOU, V. P. Wound healing properties of naphthaquinone pigments from *Alkanna tinctoria*. Experientia **34**: 1499-1501. 1978. [Alkannin esters of some acids are the active healing principles.]
- . Naturally occurring isohexenylnaphthazarin pigments: a new class of drugs. Pl. Med. **38**: 193-203. 1980. [Alkannins of the Boraginaceae; types, structure, biosynthesis, biological effects.]
- PARK, C. U. Study of the secondary xylem in herbaceous dicotyledons. I. Boraginaceae, Cruciferae, and Euphorbiaceae. Trans. Missouri Acad. Sci. **16**: 25-35. 1982. [*Cryptantha*, *Echium*, *Heliotropium*, *Lappula*, *Onosmodium*.]
- PATEL, R. C., K. N. SHENOY, & J. A. INAMDAR. Taxonomic bearing of stomatal structure and development in some Polemoniales. Feddes Report. **93**: 99-118. 1982. [Including five species of *Cordia*, *Ehretia*, and *Heliotropium*.]
- PAWLOWSKI, B. Annotationes de Pulmonariis. (In Latin.) Acta Soc. Bot. Polon. **31**: 229-238. 1962. [Interspecific hybridization; genus divided into four series.]
- . De genere *Procopiana* Guşuleac. (In Latin; Polish summary.) Fragm. Fl. Geobot. **17**: 39-58. 1971. [Three species; intergeneric hybrids; generic relatives.]
- PAYSON, E. B. A monograph of the section *Oreocarya* of *Cryptantha*. Ann. Missouri Bot. Gard. **14**: 211-358. pls. 25-30. 1927. [Forty-six species; evolutionary trends, sectional classification, taxonomy, illustrations; see MACBRIDE (1916) and HIGGINS (1971).]
- PEDERSEN, E. Pyrrolizidine alkaloids in Danish species of the Boraginaceae. Arch. Pharm. Chem. Sci. Ed. **3**: 55-64. 1975.*
- PÉREZ-MOREAU, R. L. Revisión del género *Cryptantha* en la Argentina (Boraginaceae). (English summary.) Darwiniana **20**: 155-188. 1976. [Thirteen species; descriptions, new taxa, illustrations, map.]
- PERRY, L. M. Medicinal plants of East and Southeast Asia: attributed properties and uses. ix + 620 pp. Cambridge (Massachusetts) and London. 1980. [Boraginaceae, 60-62; *Carmona*, *Cordia*, *Ehretia*, *Heliotropium*, *Lithospermum*, *Tournefortia*.]
- PHILIPP, M., & O. SCHOU. An unusual heteromorphic incompatibility system. Distyly, self-incompatibility, pollen load and fecundity in *Anchusa officinalis* (Boraginaceae). New Phytol. **89**: 693-703. 1981. [Including a brief account on occurrence of distyly in the Boraginaceae.]
- PITOT, A. Le fruit de quelques Ehrétiées. Bull. Soc. Bot. France **86**: 325-332. 1939. [*Bourreria*, *Ehretia*.]
- PLACIOS-CHÁVEZ, R., & B. LUDLOW-WIECHERS. Catálogo palinológico para la flora de Veracruz. No. 25. Familia Boraginaceae. Género *Ehretia*. (English summary.) Biotica **10**: 281-288. 1985. [Pollen heterocolpate-tricolporate, three shorter pseudocolpae alternating with true colpae.]
- & D. L. QUIROZ-GARCÍA. Catálogo palinológico para la flora de Veracruz. No. 29. Familia Boraginaceae. Género *Macromeria*. (English summary.) *Ibid.* 363-367. 1985. [Pollen penta- or hexacolporate and zonoporate, with gemmate exine.]
- POUVIER, V. Sur la recherche du bornésitol chez les Rhamnacées, Boraginacées et quelques autres familles. Compt. Rend. Acad. Sci. Paris **247**: 2190-2192. 1958. [Survey of many species of three subfamilies of Boraginaceae.]

- POLLARD, C. J., & K. S. AMUTI. Fructose oligosaccharides: possible markers of phylogenetic relationships among dicotyledonous plant families. *Biochem. Syst. Ecol.* 9: 69–78. 1981. [Five species of Ehretiaceae lack fructose oligosaccharides and fructans, 71; 19 species of Boraginaceae contain isokestose and a series of higher inulin oligosaccharides, 75.]
- POPOV, M. G. *Heliotropioideae asiatskoi tschasti SSR*. *Acta Hort. Petrop.* 42(2): 210–247. 1931.*
- . *De genere Rindera florum URSS*. (In Russian.) *Notul. Syst. Leningrad* 13: 212–227. 1950.
- . *Ad cognitionem meliorem generis Onosma L.* (In Russian.) *Ibid.* 14: 287–304. 1951a. [New species; key in Russian and Latin to the 34 species growing in USSR.]
- . *Genera nova Asiae Mediae ex tribu Eritrichieae, Boraginaceae*. (In Russian.) *Ibid.* 336–342. 1951b. [*Stephanocaryum* and *Tianschaniella*, new monotypic genera.]
- . *Boraginaceae*. In: B. K. SHISHKIN, ed., *Fl. URSS* 19: 97–691, 703–718. 1953. [English translation by R. LAVOOTT (Jerusalem), 19: 73–508, 516–531. 1974.]
- POPOVA, T. N., & E. A. ZEMSKOVA. Karyosystematics of the genus *Onosma* (Boraginaceae). *Bot. Zhur.* 70: 199–205. 1985. [New chromosome counts and review of previous reports; 30 species.]
- PRIOR, P. V. Development of the helicoid and scorpioid cymes in *Myosotis lara* Lehm. and *Mertensia virginica* L. *Proc. Iowa Acad. Sci.* 67: 76–81. 1960. [Helicoid cymes develop from the continuous renewal of meristematic activity on one side, whereas scorpioid cymes result from renewed, stepwise meristematic activity at 90 degrees from the previous flower primordium.]
- PROCTOR, G. R. *Flora of the Cayman Islands*. *Kew Bull. Add. Ser.* 11. ix + 3 maps + 834 pp. London. 1984. [Boraginaceae, 654–669.]
- KAISER, M. *Boraginaceae*. In: S. M. H. JAFRI & A. EL-GADI, eds., *Fl. Libya* 68: 1–95. 1979.
- QUIROZ-GARCÍA, D. L., & R. PALACIOS-CHÁVEZ. Catálogo palinológico para la flora de Veracruz. No. 23. Familia Boraginaceae. Género *Cryptantha*. (English summary.) *Biotica* 10: 211–213. 1985. [Pollen heterocolpate, i.e., tricolporate with three, short, true colpae alternating with pseudocolpae.]
- & ———. Catálogo palinológico para la flora de Veracruz. No. 31. Familia Boraginaceae. Género *Rochefortia*. (English summary.) *Ibid.* 11: 47–50. 1986. [*R. Lundellii*.]
- QUISUMBING, E. *Medicinal plants of the Philippines*. iv + 1262 pp. Quezon City, Philippines. 1978. [Boraginaceae, 769–780, 1256; *Coldenia*, *Cordia*, *Ehretia*, *Heliotropium*, *Rotula*, *Tournefortia*, *Trichodesma*.]
- QURESHI, U. S., & K. M. KHAN. Anomaly in pollen apertures of *Coldenia procumbens* (Boraginaceae). *Pakistan Jour. Bot.* 17: 115–117. 1985. [Pollen 6-heterocolporate instead of the previously reported 3-porate and 3-colporate.]
- & M. KAISER. Palynological study of *Onosma* (Boraginaceae) from Pakistan. *Ibid.* 19: 99–105. 1987. [Nine species; pollen 3-colporate, echinate-granulate.]
- RAFFAF, R. F. *A handbook of alkaloids and alkaloid-containing plants*. Unnumbered pages. New York, London, Sydney, and Toronto. 1970. [Alphabetical arrangement of entries that include plant families, alkaloid-names, genera, molecular formulae and weights, structure, and bibliography.]
- RECHINGER, K. H. *Zur Kenntnis der europäischen Arten der Gattung Alkanna*. *Ann. Naturhist. Mus. Wien* 68: 191–220. 4 pls. 1965. [Seventeen species and one interspecific hybrid; maps, illustrations of flowers and fruits.]
- RECORD, S. J., & R. W. HESS. *American woods of the family Boraginaceae*. *Trop. Woods* 67: 19–33. 1941. [*Auxemma*, *Bourreria*, *Cordia*, *Ehretia*, *Patagonula*, *Rochefortia*, *Tournefortia*.]

- & ———. Timbers of the New World. *Frontisp.* + xv + 640 pp. 1943. [Boraginaceae, 98–105; account is a reprint of RECORD & HESS (1941).]
- & C. D. MELL. Timbers of tropical America. *Frontisp.* + xviii + 610 pp. New Haven. 1924. [Boraginaceae, 515–524; including *Auremma*, *Cordia*, *Patagonula*.]
- REED, C. F. Economically important foreign weeds[:] potential problems in the United States. U.S. Dep. Agr., Agr. Handb. 498. 746 pp. 1977. [Boraginaceae, 496–513.]
- REHDER, A. Manual of cultivated trees and shrubs hardy in North America. ed. 2. xxx + 996 pp. New York. 1940. [Boraginaceae, 800–802; *Ehretia*, *Lithospermum*, *Moltkia*.]
- REVEDIN, P. Studio sopra i peli delle Borraginacee. Nuovo Giorn. Bot. Ital. II. 9: 301–318. 1902. [Trichome types of 27 species.]
- REICHE, C. Flora de Chile. Vol. 5. 463 pp. Santiago. 1910. [Boraginaceae, 185–240.]
- REIS, S. VON, & F. J. LIPP, JR. New plant sources for drugs and foods from the New York Botanical Garden Herbarium. *Frontisp.* + 363 pp. Cambridge, Massachusetts. 1982. [Boraginaceae, 247–249.]
- RENDLE, A. B. The classification of flowering plants. Vol. 2. xix + 636 pp. Cambridge, England. 1925. [Boraginaceae, 494–500.]
- RICHARDSON, A. T. Reinstatement of the genus *Tiquilia* (Boraginaceae: Ehretioideae) and descriptions of four new species. *Sida* 6: 235–240. 1976. [*Coldenia* reduced to a monotypic genus restricted to the Old World; many new combinations and four new species in *Tiquilia*.]
- . Monograph of the genus *Tiquilia* (*Coldenia*, *sensu lato*), Boraginaceae: Ehretioideae. *Rhodora* 79: 467–572. 1977. [Twenty-seven species in two subgenera and seven sections in the New World; generic relationships, chromosome numbers, phylogeny; maps, illustrations.]
- RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 2. New York. 1966. [Boraginaceae, 420–426, pls. 154–157; *Amsinckia*; *Cynoglossum*, *Echium*, *Hackelia*, *Heliotropium*, *Lithospermum*, *Mertensia*, *Myosotis*, *Plagiobothrys*, *Onosmodium*, *Symphytum*.]
- RIDLEY, H. N. The dispersal of plants throughout the world. *Frontisp.* + xx + 744 pp. + xxii pls. Kent, England. 1930. [Boraginaceae, 218, 300, 301, 572, 573, 594, 595, 603; pertinent information (see index) on *Borago*, *Cordia*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lithospermum*, *Mertensia*, *Myosotis*, *Symphytum*, and *Tournefortia*.]
- RIEDL, H. Die neue Borraginaceengattung *Choriantha* und ihre Stellung im Verwandtschaftskreis von *Onosma*. (English summary.) *Österr. Bot. Zeitschr.* 108: 399–407. 1961.
- . Die einjährigen Arten der Gattung *Arnebia* Forsk. *Ibid.* 109: 45–80. 1962a. [Sixteen species in two subgenera and two sections.]
- . Beiträge zur Kenntnis der Gattung *Onosma* in Asien. *Ibid.* 213–249. 1962b.
- . Bemerkungen über neue oder kritische Borraginaceen der asiatischen Flora. *Ibid.* 110: 510–542. 1963a.
- . *Anchusa* subgen. *Chamanchusa* subgen. nov. und das System der Borraginoideae–Anchuseae. *Ibid.* 543–546. 1963b. [Key to the 14 genera of tribe Anchuseae.]
- . *Decalepidanthus*, eine neue Borraginaceen-Gattung aus NW-Pakistan. *Ibid.* 608–612. 1963c. [Genus monotypic, assigned to the tribe Lithospermeae of the Borraginoideae.]
- . Boraginaceae. In: M. KØIE & K. H. RECHINGER, eds., *Symbolae Afghanicae*. Biol. Skr. Dansk Vid. Selsk. 13(4): 183–252. 1963d.
- . Ergänzende Bemerkungen zur Kenntnis von *Arnebia* Forrsk. *Österr. Bot. Zeitschr.* 111: 149–153. 1964. [*Macrotomia* reduced to a subgenus of *Arnebia*.]

- . Boraginaceae. In: K. H. RECHINGER, ed., *Fl. Iranica* 48: 1–281. 48 pls. 1967. [Forty-six genera and 336 species.]
- . Die neue Tribus Trigonotideae und das System der Boraginoideae. (English summary.) *Österr. Bot. Zeitschr.* 115: 291–321. 1968. [Tribal and subtribal limits and relationships of the Boraginoideae; tribe Trigonotideae divided into four subtribes.]
- . Die Gattung *Adelocaryum* Brand. (English summary.) *Ibid.* 119: 68–73. 1971a. [Species of *Adelocaryum* recognized as members of *Cynoglossum* and *Lindelofia*; see MILL, 1986b.]
- . Übersicht über die ausdauernden und zweijährigen Arten der Gattung *Arnebia* Forssk. *Ann. Naturhist. Mus. Wien* 75: 209–222. 1971b. [Seventeen species in two subgenera and four sections.]
- . *Cynoglossopsis somaliensis*, sp. nov., und die Gattung *Cynoglossopsis* Boraginaceae. *Pl. Syst. Evol.* 138: 283–286. 1981. [Genus of two species endemic to Ethiopia and Somalia.]
- ROBYNS, W. Outline of a new system of orders and families of Sympetaleae. *Bull. Jard. Bot. Natl. Belg.* 42: 363–372. 1972. [Boraginaceae in the order Verbenales that also includes the Hydrophyllaceae, Cordiaceae, Verbenaceae, and Labiatae.]
- ROMUSSI, G., G. FALSONE, A. E. G. CREA, & E. FINNER. Constituents of Boraginaceae 4. Anchusosidae 3. A new triterpene saponin from *Anchusa officinalis*. *Arch. Pharm. Weinheim* 316: 499–504. 1983.
- ROTH, I. Estructura anatómica de la corteza de algunas especies arbóreas venezolanas de Boraginaceae. (English summary.) *Acta Biol. Venez.* 8: 131–153. 1973. [Cortex anatomy of five species of *Cordia* and one of *Lepidocordia*.]
- . Fruits of angiosperms. *Handb. Pflanzenanat.* Vol. 10, part 1. xvi + 675 pp. 1977. [Boraginaceae, 330–336.]
- . Structural patterns of tropical barks. *Ibid.* Vol. 9, part 3. xvi + 609 pp. 1981. [Boraginaceae, 338–340, 410.]
- ROULEAU, E. Guide to the generic names appearing in the Index Kewensis and its fifteen supplements. 485 + 20 unnumbered pp. Quebec, Canada. 1981. [Boraginaceae, 324–326; Ehretiaceae, 356, 357.]
- ROYEN, P. VAN. *Sertulum Papuanum* 20. The Boraginaceae of the alpine regions of New Guinea. *Pacific Sci.* 29: 79–98. 1975. [*Crucicaryum*, *Cynoglossum*, *Myosotis*, *Trigonotis*.]
- SADAT, F. Revision ausgewählter kritischer Gattungen der Boraginaceen aus der Flora Afghanistans. *Mitt. Bot. Staatssam. München.* 28: 1–210. 1989. [Keys, descriptions, distributions, maps, illustrations.]
- SAHAY, S. K. Palynotaxonomy of Boraginaceae and some other families of Tubiflorae. *Biol. Mem. India* 4: 117–205. 6 pls. 1979. [Pollen of 174 species in some “60” genera of the Boraginaceae; evolutionary trends, importance of pollen in assessing relationships within the family and among related families; study based on light microscopy.]
- SARGENT, C. S. *Manual of the trees of North America (exclusive of Mexico)*. ed. 2. xxvi + 910 pp. Boston and New York. 1922. [Boraginaceae: *Bourreria*, *Cordia*, *Ehretia*, 858–863.]
- SATYAVATHI, D. V. L., & L. L. NARAYANA. Chemotaxonomy of some Boraginaceae. *Jour. Econ. Taxon. Bot.* 11: 95–101. 1987. [Twelve species; *Coldenia*, *Cordia*, *Ehretia*, *Heliotropium*, *Trichodesma*; tests for occurrence of 20 types of compounds, including flavonoids, alkaloids, phenols, steroids, and triterpenes.]
- SAUER, W. Karyo-systematische Untersuchungen an der Gattung *Pulmonaria* (Boraginaceae): Chromosomen-Zahlen, Karyotyp-Analysen und allgemeine Hinweise auf die Entwicklungsgeschichte. (English summary.) *Biblioth. Bot.* 131. 85 pp. 1975. [Extensive cytogeography of species and hybrids, karyology, phylogeny.]

- . The *Pulmonaria dacica* group: its affinities with central and south-east European allies and with the genus *Paraskevia* (Boraginaceae). *Pl. Syst. Evol.* **155**: 257–276. 1987. [Morphology, karyology, distribution.]
- & G. SAUER. *Paraskevia* gen. nov. mit *P. cesatiana* comb. nov. (Boraginaceae), eine endemische Gattung Griechenlands. (English summary.) *Phyton Austria* **20**: 285–306. 4 pls. 1980. [Monotypic; morphology, karyology, differences and relationships to closely related genera such as *Anchusa*, *Nonea*, *Pulmonaria*, and *Symphytum*.]
- SCHAEFER, H. Die Hohlschuppen der Boraginaceen. *Bot. Jahrb.* **72**: 303–346. 2 maps + pls. 5–7. 1942. [Morphology and anatomy of the corolla-throat scales; taxonomic value, usefulness in assessing evolutionary relationships, importance in pollination biology; survey of 462 species in numerous genera.]
- SCHÖU, O., & M. PHILIPP. An unusual heteromorphic incompatibility system. 3. On the genetic control of distyly and self-incompatibility in *Anchusa officinalis* L. (Boraginaceae). *Theor. Appl. Genet.* **68**: 139–144. 1984. [Distyly and self-incompatibility unlinked.]
- SCHUMANN, K. Untersuchungen über das Borragoid. *Ber. Deutsch. Bot. Ges.* **7**: 53–80. pl. 4. 1889. [Development of the inflorescence and flowers.]
- SCOGGAN, H. J. The flora of Canada. 4 vols. 1711 pp. Ottawa. 1979. [Boraginaceae **4**: 1276–1294.]
- SCOTT, J. K., & K. F. KENNEALLY. The distribution of Boraginaceae in western Australia in relation to the biological control of *Echium plantagineum* L. *West. Austral. Herb. Res. Notes* **5**: 81–109. 1981. [Distribution maps for 55 native and naturalized species.]
- SEIBERT, J. Fruchtanatomische Untersuchungen an Lithospermeae (Boraginaceae). *Dissert. Bot.* **44**. 207 pp. 10 pls. Vaduz. 1978. [Detailed anatomy of the nutlet wall of 37 genera, including *Buglossoides*, *Echium*, *Lithospermum*, *Mertensia*, *Myosotis*, and *Onosmodium*; anatomy of representatives of four tribes of the Boraginoideae.]
- SHARP, A. J., R. E. SHANKS, H. L. SHERMAN, & D. H. NORRIS. A preliminary checklist of dicots in Tennessee. 114 pp. Mimeographed. Univ. Tennessee, Knoxville. 1960. [Boraginaceae, 79, 80.]
- SHMIDA, A. Relationships between *Paracaryum intermedium* and *P. Boissieri* on Sinai, and the generic separation of *Paracaryum* and *Mattiastrum* (Boraginaceae). *Pl. Syst. Evol.* **129**: 323–326. 1978. [Flattened vs. inflexed fruit wing, found in plants of one species, may not be useful for the separation of *Mattiastrum* from *Paracaryum*.]
- SHREVE, F., & I. L. WIGGINS. Vegetation and flora of the Sonoran Desert. Vol. 2. v + pp. 841–1740. Stanford. 1964. [Boraginaceae, 1202–1234.]
- SHUKLA, Y. N., J. S. TANDON, D. S. BHAKUNI, & M. M. DHAR. Naphthoquinones of *Arnebia nobilis*. *Phytochemistry* **10**: 1909–1915. 1971. [Isolation and characterization of several new alkannins with anticancer and antibiotic activities.]
- SINGH, T. C. N. Studies in the morphology of pollen grains. —1(a) Boraginaceae. *Jour. Indian Bot. Soc.* **10**: 38–42. pl. 1931. [*Anchusa*, *Borago*, *Gastrocotyle*, *Heliotropium*, *Myosotis*, *Nonea*.]
- SMALL, J. K. Flora of the southeastern United States. xii + 1370 pp. New York. 1903. [Boraginaceae, 995–1002; Ehretiaceae, 1002–1004; Heliotropiaceae, 1004–1007.]
- . Shrubs of Florida. x + 140 pp. New York. 1913. [Ehretiaceae, 113, 114; *Bourreria* and *Cordia* (as *Sebesten* and *Varronia*). Heliotropiaceae, 114, 115; *Heliotropium*, *Tournefortia*.]
- . Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. [Boraginaceae, 1121–1128; Ehretiaceae, 1128–1130; Heliotropiaceae, 1130–1134.]
- SMIRNOVA, S. A. A key to genera of Boraginaceae weeds in the USSR according to organs remaining on plants during fruit bearing. *Biol. Nauki Mosk.* **1983**(3): 61–66. 1983.*

- SMITH, E. B. An atlas and annotated list of vascular plants of Arkansas. iv + 592 pp. Fayetteville, Arkansas. 1978. [Boraginaceae, 23-27, 515, 525; county distributions, chromosome numbers, common names, notes.]
- . An atlas and annotated list of vascular plants of Arkansas. ed. 2. iv + 489 pp. Fayetteville, Arkansas. 1988. [Boraginaceae, 17-21.]
- SMITH, L. B. Boragináceas. In: P. R. REITZ, Fl. Illustr. Catarinense. 85 pp. Itajai, Brazil. 1970. [*Cordia*, *Cynoglossum*, *Heliotropium*, *Myosotis*, *Tournefortia*.]
- SMITH, L. W., & C. C. J. CULVENOR. Plant sources of hepatotoxic pyrrolizidine alkaloids. Jour. Nat. Products **44**: 129-152. 1981. [Boraginaceae, 130-133, 140.]
- SMITH, S. G. Cytology of *Anchusa* and its relation to the taxonomy of the genus. Bot. Gaz. **94**: 394-403. 1932. [Cytological data support previous taxonomic conclusions regarding the generic limits and sectional divisions of *Anchusa*.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez *l'Omphalodes linifolia* Moench. Compt. Rend. Acad. Sci. Paris **247**: 249-253. 1958a.
- . Embryogénie des Boragacées. Développement de l'embryon chez *l'Echinospermum Lappula* Lehm. Ibid. 761-766. 1958b.
- STANDLEY, P. C. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. **23**: 1-1721. 1920-1926. [Boraginaceae, 1216-1234. 1924; *Bourreria*, *Coldenia*, *Cordia*, *Ehretia*, *Heliotropium*, *Tournefortia*.]
- STEARNS, W. T. Taxonomic and nomenclatural notes on Jamaican gamopetalous plants. Jour. Arnold Arb. **52**: 614-648. 1971. [Boraginaceae, 619-634; *Bourreria*, *Cordia*, *Tournefortia*.]
- STEBBINS, G. L. Flowering plants: evolution above the species level. xviii + 399 pp. Cambridge, Massachusetts. 1974. [Boraginaceae, 353; questionably belong to the Polemoniales.]
- STEYERMARK, J. A. Flora of Missouri. lxxxiii + 1725 pp. Ames, Iowa. [1963]. [Boraginaceae, 1242-1257.]
- STRAUSBAUGH, P. D., & E. L. CORE. Flora of West Virginia. ed. 2. xl + 1079 pp. Grantsville, West Virginia. 1978. [Boraginaceae, 777-785.]
- STREY, M. Karyologische Studien an Boraginoideae. Planta **14**: 682-730. 1931. [The first comprehensive cytological study of the subfamily; numerous new chromosome counts from somatic and meiotic cells, base chromosome numbers, pollen development; 53 species in 18 genera, including *Amsinckia*, *Borago*, *Cynoglossum*, *Echium*, *Lappula*, *Lithospermum*, *Lycopsis*, *Myosotis*, and *Symphytum*.]
- STROH, G. Die Gattung *Onosma* Linn. Versuch einer systematischen Kodifizierung der Arten. Beih. Bot. Centralbl. **59B**: 430-454. 1939. [Three sections and 128 species; checklist, types of species and infraspecific taxa.]
- SUFFNESS, M., & G. A. CORDELL. Antitumor alkaloids. In: A. BROSS, ed., The alkaloids: chemistry and pharmacology. **25**: 1-369. 1985. [Pyrrolizidine alkaloids, 21-38; species of Boraginaceae and of other families.]
- SVENSSON, H. G. Zur Embryologie der Hydrophyllaceen, Boraginaceen und Heliotropiaceen. Uppsala Univ. Årsskr. Math. Naturv. **2**. 176 pp. + 3 pls. 1925. [Megaspороgenesis, endosperm and embryo development of numerous taxa.]
- SYNGE, P. M., ed. Dictionary of gardening. ed. 2. 4 vols. Oxford. 1965. (Supplement 1969.) [Boraginaceae, 298; listing of 41 genera, treated alphabetically.]
- TAKHTAJAN, A. Flowering plants: origin and dispersal. (English translation from Russian by C. JEFFREY.) x + 310 pp. Edinburgh. 1969. [Boraginaceae in the Polemoniales, 231.]
- . Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46**: 225-359. 1980. [Boraginaceae placed with the Hydrophyllaceae, Lennoaceae, and Hoplestigmataceae in suborder Boraginineae of the Polemoniales, 294, 295.]

- . *Systema magnoliophytorum*. (In Russian.) 439 pp. Leningrad. 1987. [Boraginales, 244–247; order includes Hydrophyllaceae, Lennoaceae, Hoplestigmataceae, Ehretiaceae, Cordiaceae, Boraginaceae, and Wellstediaceae; Boraginaceae divided into subfamilies Boraginoideae and Heliotropioideae.]
- TARNAVSCHI, I. T. Études caryo-systématiques sur le genre *Pulmonaria* L., basées sur la morphologie des chromosomes et la méiose. (In Rumanian; French summary.) *Bul. Facul. Stiinte Cernăuți* 9: 47–122. 1935. [Thirteen species and seven putative hybrids; haploid and diploid chromosome numbers, karyotypes.]
- TAYLOR, L. A. Plants used as curatives by certain southeastern tribes. xi + 88 pp. Cambridge, Massachusetts. 1940. [Boraginaceae, 52; *Cynoglossum virginicum*, *Hackelia* (as *Lappula*) *virginica*.]
- TEPPNER, H. Cytosystematik, bimodale Chromosomensätze und permanente Anorthoploidie bei *Onosma* (Boraginaceae). (English summary.) *Österr. Bot. Zeitschr.* 119: 196–233. 1971a. [Twenty-four species; taxonomic notes, nomenclature, hybridization, chromosome numbers.]
- . Cytosystematische Studien an *Onosma* (Boraginaceae). Die Formenkreise von *O. echioides*, *O. helveticum* und *O. arenarium*. (English summary.) *Ber. Deutsch. Bot. Ges.* 84: 691–696. 1971b. [Allotetraploidy.]
- . Karyosystematik einiger asiatischer *Onosma*-Arten (Boraginaceae), inkl. *O. interspectatum* Teppner, sp. nov. (English summary.) *Pl. Syst. Evol.* 123: 61–82. 1974. [Karyotypes of seven species.]
- TÉTÉNYI, P. Données chimiotaxinomiques sur les Boraginacées. (English summary.) *Acta Bot. Acad. Sci. Hungar.* 20: 159–167. 1974. [Fatty acids of 40 species; relevance of data in the infrafamilial subdivisions of the Boraginaceae.]
- THORNE, R. F. A phylogenetic classification of the Angiospermae. Pp. 35–106 in M. K. HECHT, W. C. STEERE, & B. WALLACE, eds., *Evolutionary biology*. Vol. 9. New York and London. 1976. [Boraginaceae placed in suborder Boraginineae with Lennoaceae and Hoplestigmataceae, 64.]
- . Proposed new realignments in the angiosperms. *Nordic Jour. Bot.* 3: 85–117. 1983. [Boraginaceae in the Solanales, 108.]
- . Phytochemistry and angiosperm phylogeny: a summary statement. Pp. 233–295 in D. A. YOUNG & D. S. SEIGLER, eds., *Phytochemistry and angiosperm phylogeny*. New York. 1981. [Boraginales, 252, 289.]
- THORSCH, J., & K. ESAU. Nuclear crystalloids in sieve elements of Boraginaceae: a protein digestion study. *Jour. Cell Sci.* 64: 37–47. 1983. [*Amsinckia*, *Echium*.]
- TIEGHEM, P. VAN. Sur les Heliotropiacées. *Ann. Sci. Nat. Bot.* IX. 4: 261–271. 1906. [The Boraginaceae *sensu lato* divided into Boraginaceae, Cordiaceae, Ehretiaceae, and Heliotropiaceae.]
- . Structure du pistil et du fruit des Labiées, des Boragacées et des familles voisines. *Ibid.* 5: 321–350. 1907. [Fruit type, ovule attachment, embryo structure, and style division at apex and insertion at base, all used to subdivide the Boraginaceae into four families; relationships to six families.]
- TISSOT-DAGUETTE, M. Recherches cytotaxonomiques sur le genre *Onosma*. (English summary.) *Bull. Soc. Bot. Suisse* 82: 291–299. 1973. [New base chromosome number (8) for the genus; interspecific hybridization.]
- . Nouvelles recherches cytotaxonomiques sur le genre *Onosma* L. (English summary.) *Compt. Rend. Acad. Sci. Paris D.* 288: 755–758. 1979. [First chromosome counts for 13 species; cytogeography.]
- TOELKEN, H. R. Boraginaceae. Pp. 1146–1173 in J. P. JESSOP & H. R. TOELKEN, eds., *Fl. South Australia*. Part 3. Adelaide, Australia. 1986. [Fourteen genera, including *Amsinckia*, *Borago*, *Buglossoides*, *Cynoglossum*, *Echium*, *Myosotis*, and *Plagiobothrys*.]
- UPHOF, J. C. T. Dictionary of economic plants. ed. 2. 591 pp. New York and Codicote (England). 1968. [*Borago*, *Cordia*, *Cynoglossum*, *Echium*, *Heliotropium*, *Lithospermum*, *Mertensia*, *Myosotis*, *Symphytum*; see for several other genera.]

- VALDÉS, B. *Gyrocaryum* Valdés, gen. novum (Boraginaceae, Erytrichieae [sic]). *Willdenowia* 13: 107-109. 1983. [Monotypic; unusual for the Erytrichieae, having opposite leaves and cartilaginous apical ring crowning each nutlet.]
- VALEN, F. VAN. Contribution to the knowledge of cyanogenesis in Angiosperms. 12. Communication. Cyanogenesis in Boraginaceae. *Proc. Ned. Akad. Wet. C.* 82: 171-176. 1979. [Negative tests of cyanogenesis in many species, review of earlier literature; *Borago* contains the cyanogenic glucoside dhurrin.]
- VALENTINE, D. H., & A. O. CHATER, eds. Boraginaceae. In: T. G. TUTIN *et al.*, eds., *Fl. Europaea* 3: 83-122. 1972.
- VASUDEVAN, K. N. Contribution to the cytotaxonomy and cytogeography of the flora of the western Himalayas (with an attempt to compare it with the flora of the Alps). Part II. *Bull. Soc. Bot. Suisse* 85: 210-252. 1975. [Boraginaceae, 210-214, 238, 239, *figs.* 36-56.]
- VENKATESWARLU, J., & B. ATCHUTARAMAMURTI. Embryological studies in Boraginaceae. I. *Coldenia procumbens* Linn. *Jour. Indian Bot. Soc.* 34: 235-247. 1955. [Mega- and microsporogenesis, embryogeny; resemblance to *Heliotropium*.]
- VENO, B. A revision of the genus *Pectocarya* (Boraginaceae) including reduction to synonymy of the genus *Harpagonella* (Boraginaceae). Unpubl. Ph. D. dissertation, Univ. California, Los Angeles. 1979.*
- VERDCOURT, B. A new genus *Nogalia* (Boraginaceae-Heliotropioideae) from Somaliland and southern Arabia. *Kew Bull.* 43: 431-435. 1988. [A monotypic genus related to *Heliotropium* and endemic to Arabia and Somalia.]
- VERESHCHAGINA, V. A. The development of endosperm in *Pulmonaria* (Boraginaceae). (In Russian.) *Bot. Zhur.* 68: 1107-1112. 1983. [Including types of endosperm development in the Boraginaceae.]
- VOYTENKO, V. F., & S. N. OPARINA. Heterocarpy in the family Boraginaceae. (In Russian; English summary.) *Bot. Zhur.* 70: 865-875. 1985. [Occurrence in *Buglossoides*, *Echium*, *Heterocaryum*, *Lappula*, and *Paracaryum*.]
- & ———. Anatomical analysis of heterocarpy in the Boraginaceae family. (In Russian; English summary.) *Ibid.* 72: 569-580. 1987. [Evolutionary trends; *Buglossoides*, *Heterocaryum*, *Lappula*.]
- VUILLEUMIER, B. S. The origin and evolutionary development of heterostyly in the angiosperms. *Evolution* 21: 210-226. 1967. [Boraginaceae, 215; *Amsinckia*, *Cordia*, *Lithospermum*, *Pulmonaria*.]
- VURAL, M., & KIT TAN. New taxa and records from Turkey. *Notes Bot. Gard. Edinburgh* 41: 65-76. 1983. [*Cynoglottis*, gen. nov., 70-75; based on *Anchusa* subg. *Cynoglottis* Guşuleac.]
- WAGENITZ, G. New aspects of the systematics of Asteridae. Pp. 375-395 in K. KUBITZKI, ed., *Flowering plants: evolution and classification of higher categories*. *Pl. Syst. Evol. Suppl.* 1. Wien. 1977. [Boraginaceae placed with the Solanaceae in the Polemoniales; the Lamiales associated with the Scrophulariales.]
- WANG, C.-J. Taxonomic and phytogeographic studies on Chinese species [of] *Trigonotis* Stev. (In Chinese; English summary.) *Acta Bot. Yunnanica* 4: 31-45. 1982. [Sectional classification, new taxa, distributions; 33 species recognized in China.]
- WANG, W.-T. A revision of the genus *Microula* (Boraginaceae). (In Chinese; English summary.) *Acta Phytotax. Sinica* 18: 266-282. 1980. [Thirty species; evolutionary trends, center of diversity, new taxa.]
- , Y.-S. LIAN, & J.-Q. WANG. A study of the genus *Eritrichium* from China. (In Chinese.) *Bull. Bot. Lab. North-East Forest Inst.* 9: 31-52. 1980a. [Forty species in two subgenera, four sections, and six series; several novelties and new combinations.]
- , ——— & ———. New taxa of Boraginaceae from Xizang (Tibet). (In Latin, with brief notes in Chinese.) *Acta Phytotax. Sinica* 18: 514-520. 1980b. [*Metaeritrichium*, gen. nov.; new taxa in *Eritrichium*.]

- WARD, D. B., & P. R. FANTZ. Keys to the flora of Florida-3, Boraginaceae. *Phytologia* 36: 309-323. 1977. [*Bourreria*, *Buglossoides*, *Cordia*, *Cynoglossum*, *Heliotropium*, *Lithospermum*, *Mallotonia*, *Myosotis*, *Onosmodium*, *Tournefortia*; keys to the species, taxonomic notes, distributions, common names.]
- WERNHAM, H. F. Floral evolution: with particular reference to the sympetalous dicotyledons. V. Tetracyclidae: Part II. Tubiflorae. *New Phytol.* 10: 293-305. 1912.
- WETTSTEIN, R. VON. *Moltkea Dörfleri* Wettstein und die Abgrenzung der Gattung *Moltkea*. *Österr. Bot. Zeitschr.* 67: 361-369. pl. 3. 1918. [Eight species in two sections.]
- WIGGINS, I. L. Boraginaceae. Pp. 277-296 in I. L. WIGGINS & D. M. PORTER, Fl. Galapagos Islands. xx + 998 pp. Stanford. 1971. [*Coldenia*, *Cordia*, *Heliotropium*, *Tournefortia*.]
- . Flora of Baja California. viii + 1025 pp. Stanford. 1980. [Boraginaceae, 213-229.]
- WIGHT, W. F. The genus *Eritrichium* in North America. *Bull. Torrey Bot. Club* 29: 407-414. 1902. [Six species.]
- WILLAMAN, J. J., & H.-L. LI. Alkaloid-bearing plants and their contained alkaloids, 1957-1968. *Lloydia* 33 (3A, supplement). vii + 286 pp. 1970. [Boraginaceae, 62, 63; alkaloids of 47 species in 21 genera.]
- & B. G. SCHUBERT. Alkaloid-bearing plants and their contained alkaloids. U.S. Dep. Agr. Tech. Bull. 1234. 287 pp. 1961. [Boraginaceae, 54-56; literature survey of 36 species in 17 genera.]
- WILLIS, J. C. A dictionary of the flowering plants and ferns. ed. 8. (Revised by H. K. AIRY SHAW.) xxii + 1245 + lxvi pp. Cambridge, England. 1973. [Boraginaceae, 150, 151.]
- WOFFORD, B. E. Guide to the vascular plants of the Blue Ridge. xiv + 384 pp. Athens (Georgia) and London. 1989. [Boraginaceae, 183-185; *Cynoglossum*, *Echium*, *Hackelia*, *Lithospermum* (including *Buglossoides*), *Mertensia*, *Myosotis*, *Onosmodium*.]
- WRÓBEL, J. T. Pyrrolizidine alkaloids. In: A. BROSSI, ed., The alkaloids: chemistry and pharmacology 26: 327-384. 1985. [Structural diversity, biosynthesis; toxicity and pharmacology of compounds from certain Boraginaceae.]
- WUNDERLIN, R. P. Guide to the vascular plants of central Florida. 472 pp. Tampa, St. Petersburg, Fort Myers, and Sarasota. 1982. [Boraginaceae, 310-312.]
- YOUNG, D. J., & L. WATSON. The classification of dicotyledons: a study of the upper levels of the hierarchy. *Austral. Jour. Bot.* 18: 387-433. 1970. [Boraginaceae and Solanaceae are perhaps close to the asclepioids, 419.]
- YOUNGKEN, H. W. Textbook of pharmacognosy. ed. 6. *Frontisp.* + xvii + 1063 pp. New York, Toronto, and London. 1950. [Boraginaceae, 700-703; *Alkanna*, *Borago*, *Symphytum*.]
- ZALKOW, L. H., S. BONETTI, L. GELBAUM, M. M. GORDON, B. B. PATIL, A. SHANI, & D. VAN DERVEER. Pyrrolizidine alkaloids from Middle Eastern plants. *Jour. Nat. Products* 42: 603-614. 1979. [Including species of *Cynoglossum*, *Heliotropium*, and *Trichodesma*.]
- ZEVEN, A. C., & J. M. J. DE WET. Dictionary of cultivated plants and their regions of diversity. 263 pp. Wageningen. 1982. [Boraginaceae, 34, 51, 88, 104, 149; *Alkanna*, *Borago*, *Lithospermum*, *Symphytum*, *Tournefortia*.]
- ZHAO, S.-D. The genus *Thyrocarpus* Hance recently discovered in N.-E. China. (In Chinese.) *Bull. Bot. Res. North-East Forest Inst.* 1(3): 78-80. 1981. [*T. glochidiatus*; genus includes three species all endemic to China, treated by MAXIMOWICZ in *Bull. Acad. Sci. St. Petersb.* 26: 499. 1880.]

KEYS TO THE SUBFAMILIES, TRIBES, AND GENERA OF BORAGINACEAE
IN THE SOUTHEASTERN UNITED STATES⁴

Herbs, shrubs, or trees; leaves simple, usually alternate, exstipulate; inflorescences bracteate or ebracteate cymes; flowers hypogynous, usually actinomorphic, perfect, usually pentamerous; calyx gamosepalous, 5 lobed; corolla sympetalous, 5 lobed, variously shaped, with or without faucal appendages; stamens epipetalous, as many as corolla lobes and alternate with them, exerted or included; gynoecium of 2 united carpels; ovary superior, deeply 4 lobed or not lobed; placentation axile or nearly basal; style gynobasic or terminal, simple or divided near apex; stigma capitate, simple or 2 or 4 lobed; fruits usually of 4 (or fewer by abortion) nutlets, sometimes 1- to 4-seeded drupe or nutlet; seeds oblique or horizontal; testa membranaceous; embryo straight or curved.

KEY TO THE SUBFAMILIES AND TRIBES

- A. Style terminal; ovary not lobed or only slightly lobed; fruit drupaceous or a schizocarp splitting at maturity into four 1-seeded nutlets; trees, shrubs or herbs.
 - B. Style twice branched, the 4 branches each terminating in a stigma; cotyledons plicate I. Subfam. CORDIOIDEAE.
 - B. Style unbranched; stigmas 1 or 2; cotyledons not plicate.
 - C. Stigmas 2, capitate, without a sterile apical portion II. Subfam. EHRETIOIDEAE.
 - C. Stigma 1, conical or frustumlike, with a conspicuous sterile distal portion III. Subfam. HELIOTROPIOIDEAE.
- A. Style gynobasic; ovary deeply 4-lobed; fruit of 4 distinct nutlets; herbs or very rarely shrubs IV. Subfam. BORAGINOIDEAE.
- D. Corolla lobes imbricate in bud; attachment scar of nutlet ventral to apical, or if basal then large and well developed.
 - E. Gynobase pyramidal or columnar, attachment scar usually ventral or apical.
 - F. Nutlets attached basally or suprabasally, usually well before the middle, not divergent basally.
 - G. Nutlets tetrahedral, not keeled ventrally, usually neither winged nor appendaged 1. Tribe TRIGONOTIDEAE.
 - G. Nutlets variously shaped, not tetrahedral, usually conspicuously keeled ventrally, often appendaged or winged 2. Tribe ERITRICHIEAE.
 - F. Nutlets attached apically or well above the middle, distinctly divergent basally 3. Tribe CYNOGLOSSEAE.
 - E. Gynobase usually flat, attachment scar of nutlets basal.
 - H. Nutlets neither strophiolate nor with a basal annular rim; gynobase without cavities 4. Tribe LITHOSPERMEAE.
 - H. Nutlets strophiolate, with a basal annular rim; gynobase with 4 cavities left by the caruncles 5. Tribe BORAGINEAE.
- D. Corolla lobes contorted in bud; attachment scar of nutlet basal, very small 6. Tribe MYOSOTIDEAE.

KEY TO THE GENERA

- A. Trees, shrubs, or woody vines; fruit drupaceous, usually fleshy.
 - B. Stigmas 4; style twice-cleft into 4 branches 1. *Cordia*.

⁴The arrangement of subfamilies, tribes, and genera follows that of Riedl (1967). Where a given genus is not included in that reference, the position follows Johnston (1924a) and/or Cronquist (1984).

- B. Stigmas 2 or 1; style undivided or once-cleft into two branches.
- C. Stigmas 2; style cleft2. *Bourreria*.
- C. Stigmas 1; style undivided.
 - D. Woody vines (ours) of different habitats; fruits fleshy; trichomes not silky3. *Tournefortia*.
 - D. Shrubs of strand habitats; fruits corky; trichomes silky, slender.....4. *Argusia*.
- A. Herbs; fruits of 1 to 4 one-seeded nutlets.
 - E. Style terminal or obsolete; stigma conical, with a sterile upper half; ovary not divided5. *Heliotropium*.
 - E. Style gynobasic; stigma without a sterile upper half; ovary deeply divided into 4 lobes.
 - F. Nutlets with glochidiate prickles.
 - G. Nutlets erect, attached to the gynobase by an elongated or broad ventral scar.
 - H. Fruiting pedicels deflexed or recurved; cymes naked or bracteate only near the base; gynobase broadly pyramidal; attachment scar of nutlet broad; plants perennial or rarely biennial.....9. *Hackelia*.
 - H. Fruiting pedicels erect or ascending; cymes bracteate; gynobase subulate; attachment scar of nutlet narrow, along ventral keel; plants usually annual.....10. *Lappula*.
 - G. Nutlets spreading or divergent, attached to the gynobase by an apical scar11. *Cynoglossum*.
 - F. Nutlets without glochidiate appendages.
 - I. Nutlets attached laterally to a pyramidal gynobase.
 - J. Corolla blue, pink, or white, throat with faucal appendages; cotyledons entire.
 - K. Plants (ours) glabrous; corolla pink to blue (rarely white), the tube much longer than the calyx; nutlets not keeled dorsally.....6. *Mertensia*.
 - K. Plants strigose or hispid; corolla white, the tube subequalling calyx; nutlets keeled dorsally7. *Plagiobothrys*.
 - J. Corolla yellow or orange, throat without faucal appendages; cotyledons deeply 2-cleft8. *Amsinckia*.
 - I. Nutlets attached basally to a flat or broadly convex, pitted or not pitted gynobase.
 - L. Attachment scar large, nutlets neither laterally compressed nor rimmed; corolla lobes imbricate in bud.
 - M. Nutlets without a basal, annular rim, not strophiolate, not leaving pits on the gynobase.
 - N. Corolla regular; stamens equal in length.
 - O. Corolla lobes rounded, spreading; style included.
 - P. Corolla yellow or orange; throat without elongated vertical bands; faucal appendages and/or stipitate glands present..12. *Lithospermum*.
 - P. Corolla blue to white; throat with 5, well-developed, elongated, vertical bands of crowded, stipitate glands or hairs13. *Buglossoides*.
 - O. Corolla lobes acute to acuminate, erect; style long-exserted..14. *Onosmodium*.
 - N. Corolla irregular; stamens unequal in length.....15. *Echium*.
 - M. Nutlets with a basal annular rim, strophiolate, leaving pits on the gynobase.
 - Q. Corolla rotate; stamens exserted, dorsally appendaged, nearly connivent and forming a cone around the style16. *Borago*.
 - Q. Corolla tubular or funneliform; stamens included, unappendaged.

- R. Corolla tubular, with well-developed, campanulate throat, the lobes short, recurved or erect; faucal appendages linear to linear-lanceolate, denticulate 17. *Symphytum*.
 R. Corolla funnelform to salverform, with poorly developed throat, the lobes large, spreading; faucal appendages oblong to deltoid, hairy [*Anchusa*.]⁵
 L. Attachment scar minute; nutlets laterally compressed, rimmed; corolla lobes contorted in bud 18. *Myosotis*.

Subfam. I. CORDIOIDEAE Gürke in Engler & Prantl, Nat. Pflanzenfam. VI. **3A**: 81. 1897.

1. *Cordia* Linnaeus, Sp. Pl. 1: 190. 1753; Gen. Pl. ed. 5. 87. 1754.

Evergreen or deciduous trees, shrubs, subshrubs [or rarely woody climbers] with watery juice, glabrous or variously pubescent or villous with unbranched or stellate trichomes. Leaves alternate [or rarely opposite], exstipulate, petiolate or subsessile, the blades entire or dentate; petioles usually sulcate on the adaxial surface. Inflorescences paniculate, spicate, capitate, glomerulate, or cymose, terminal or axillary, ebracteate [rarely bracteate]. Flowers regular (actinomorphic), perfect [or imperfect and the plants dioecious], pedicellate or sessile. Calyx campanulate [to tubular], 2-5 (-10) lobed, opening with teeth [or rarely circumscissile], persistent, usually accrescent, at maturity subtending or enclosing the fruit. Corolla campanulate, funnelform (or tubular), 4 or 5 (-8) lobed, white, cream, yellow, orange, or red, usually glabrous, caducous [or persistent and aiding in fruit dispersal]; lobes plicate, imbricate, or rarely contorted in bud, spreading to reflexed, rarely obsolete and the corolla undulate to truncate at apex. Stamens as many as the corolla lobes, epipetalous, exserted or included; filaments usually pubescent at or near the area of adnation to the corolla tube; anthers oblong, ovoid, ellipsoid or linear, sagittate or hastate at base. Ovary not lobed, sessile, 4 loculate, subtended by an annular to crateriform disc; style terminal, twice bifid; stigmas 4, filiform, clavate, or discoid. Fruits fleshy, white, green, yellow, orange, or red drupes with a thin exocarp, mucilaginous to juicy mesocarp, and bony endocarp [or dry with either a bony pericarp or a fibrous one capped by the cartilaginous persistent base of style], symmetrical or asymmetrical, glabrous or pubescent. Seeds 1 or very rarely 2; cotyledons thick and fleshy or membranaceous and usually longitudinally plicate, shorter than the radicle. Base chromosome numbers 7-10. (Including *Acnadena* Raf., *Borellia* Necker, *Catonia* Raf., *Cerdana* Ruiz & Pavón, *Coilanthera* Raf., *Collococcus* P. Browne, *Cordiada* Vellozo, *Ectemes* Raf., *Firensia* Scop., *Gerascanthus* P. Browne, *Hymenesthes* Miers, *Lithocardium* Kuntze, *Montjolya* Friesen, *Myxa* (Endl.) Lindley, *Paradigma* Miers, *Physoclada* (DC.) Lindley, *Pilicordia* (A.

⁵As indicated above, *Anchusa* was reported once from Tennessee and has not been treated for this flora.

DC.) Lindley, *Piloisia* Raf., *Plethostephia* Miers, *Rhabdocalyx* (A. DC.) Lindley, *Sebesten* Adanson, *Sebestena* Boehmer, *Topiaris* Raf., *Toquera* Raf., *Ulmarronia* Friesen, *Varroa* Cothenius, *Varronia* P. Browne, *Varroniopsis* Friesen.) LECTOTYPE SPECIES: *C. Myxa* L.; see Britton, North American trees. 819. 1908.⁶ (Name commemorating Valerius Cordus, 18 Feb. 1515–25 Sept. 1544, a German physician and botanist.)

A pantropical genus, the largest of the Boraginaceae, with more than 320 species, including at least 20 described during the past three years. The majority of the species are centered in the New World tropics and subtropics. There are about 90–100 species (80 percent endemic) in the West Indies (my compilation), some 65 in Brazil (Taroda & Gibbs, 1986a), 61 in Central America (Miller, 1985a), 42 in Venezuela (Gaviria), and 30 species in Peru (Macbride, 1960). *Cordia* is also well

⁶The typification of *Cordia* is controversial, and each of the three original Linnaean species (*C. Myxa*, *C. Sebestena*, and *C. glabra*) (Linnaeus, Sp. Pl. 1: 190. 1753) has been chosen as a lectotype. All recent studies of the genus (e.g., Gaviria; Johnston 1930, 1951a; Miller, 1985a, 1988; Taroda & Gibbs, 1986; Warfa, 1988a), as well as Farr *et al.*, have followed Hitchcock & Green in accepting *C. Sebestena* as the lectotype. As shown by Wood, however, Hitchcock & Green overlooked most of the earlier typifications, particularly those of Britton and his coworkers. Johnston (1930) presented a strong argument in support of *C. Sebestena* as the lectotype of the genus, but later (1951a) he changed his opinion and stated (p. 3) that "Logic may demand that *C. Sebestena* be accepted as genotype, but I have come to realize the possible effects, and now believe logic should yield to expediency. *Cordia Sebestena* is one of a small group of mainly West Indian species, certainly aberrant in *Cordia* as a whole, which has been and probably should be treated as generically distinct. I am not prepared to have the name *Cordia* restricted to the few relatives of *C. Sebestena*. It seems best to have *C. Myxa* declared the genotype of *Cordia* and so guarantee the continued wide application of the epithet." Warfa (1988a) suggested that the typification problems could be solved by conserving *Cordia* with a new type. In fact, Nowicke & Ridgway have already recommended that *C. Myxa* be conserved as the type but no formal proposal has been made.

Johnston's (1951a) argument for replacing *C. Sebestena* by *C. Myxa* as the lectotype could be considered contradictory to the current rules of botanical nomenclature (see ICBN, Article 8. 1988) only if *C. Sebestena* was the first chosen lectotype. However, this is not the case, and Hitchcock & Green were the last to typify the genus. Britton & Wilson (1925), who recognized several segregates of *Cordia*, selected *C. glabra* as the type, but Miller (1985a) indicated that the species is now considered to belong to *Bourreria*. The third Linnaean species, *C. Myxa*, was chosen as the type by Britton in his North American Trees. This is the earliest typification of *Cordia*. Some authors believe that Britton and his coworkers followed a mechanical procedure in the lectotypification of genera, and that they selected the first of the Linnaean species (Sp. Pl. ed. 1. 1753) as the generic lectotype. However, their lectotypifications were usually carefully done, and in numerous instances they did not necessarily choose the first species. A case in point is Britton & Brown's (Illus. Fl. No. U.S. & Canada. ed. 2. 2: 335. 1913) lectotypification of the genus *Cassia* L., in which they selected as a lectotype *C. fistulosa* L., the twelfth of 26 species enumerated by Linnaeus (Sp. Pl. 1: 377. 1753).

The acceptance of *C. Myxa* as the generic lectotype negates the need to typify the genus with a conserved type. The few nomenclatural adjustments that need to be made at the sectional rank will be only minor, and sect. *Cordia*, as lectotypified by *C. Myxa*, represents the major portion of the genus. Such lectotypification should add considerable nomenclatural stability to *Cordia*, no matter how the genus is subsequently subdivided.

represented in Bolivia, Colombia, and Ecuador, but the total number of species in these countries is not accurately known. By contrast, the genus is poorly represented in the paleotropics, where only about 40–50 species grow (my compilation from Baker & Wright; Corner; Heine; Johnston, 1951a; Taton; and Warfa, 1988a). *Cordia* is represented in the southeastern United States by two indigenous species, as well as by seven cultivated ornamentals, all of which grow in Florida.

Cordia is most closely related to the South American *Auxemma* Miers (two to four species; Brazil) and *Patagonula* L. (two species; Argentina, Bolivia, Brazil, and Paraguay). The three genera together form the subfamily Cordioideae. *Auxemma* differs from *Cordia* in having a dry, broadly winged, accrescent calyx, whereas *Patagonula* is easily distinguished from these two in having persistent, winglike calyx lobes that are distinct almost to the very base (Gürke). In this respect, *Patagonula* resembles superficially members of the Dipterocarpaceae.

The limits of *Cordia* have been controversial; Friesen divided the genus into ten segregates, while others (e.g., Nowicke & Ridgway) have suggested elevating three sections to generic rank. Perhaps the most problematic aspect of *Cordia* is the infrageneric classification. Students of the genus prior to 1930 have recognized a few to many sections on the basis of poorly studied characters.

The infrageneric classification adopted here, as well as that followed in the works of Gaviria, Miller (1985a), Taroda & Gibbs (1986a, 1986b, 1987), and Warfa (1988a), is based on Johnston's (1930, 1940, 1949, 1950, 1951a) painstaking studies of *Cordia*. Johnston, who is credited with more than 50 binomials in the genus, relied heavily on the shape, size, and persistence of the perianth, the type and shape of the inflorescence, and the various features of the fruit in defining sectional boundaries in the genus. Although over the years he proposed a few adjustments to his earlier sectional classification (Johnston, 1930), the work as a whole remains a solid foundation on which later studies are based.

Nowicke & Ridgway proposed to divide *Cordia* into three genera primarily on the basis of palynological data that are also well supported by certain aspects of fruit or inflorescence morphology. They suggested that sect. *Varronia* (Browne) Cham. be elevated to a genus because it uniquely differs from the rest of *Cordia* in having 3-porate grains with reticulate sexine and glomerulate, globose, or spikelike cymose inflorescences in which the terminal flower matures first. They also proposed that sect. *Sebestenae* G. Don (as sect. *Cordia*) be raised to generic rank and that it is characterized by having 3-colpate or 3-colporoidate pollen with a striate-reticulate sexine, paniculate inflorescence, and an enlarged calyx that encloses the whole fruit. The remaining bulk of *Cordia*, which has 3-colpate to 3-colporate grains with a spinulose sexine, was considered by Nowicke & Ridgway to be a coherent third genus.

Nowicke & Ridgway's careful studies on the pollen of *Cordia* have been confirmed by subsequent workers (e.g., Tarada & Gibbs, 1986a; Palacios-Chávez & Quiroz-García), and they provide a solid foundation

on which the infrageneric classification of the genus is based. In fact, Miller and Nowicke utilized pollen data, as well as those of the fruit and corolla, to solve the problematic sectional disposition of several species of *Cordia*. However, their interpretation of sect. *Cordia* is different from mine because they accepted *C. Sebestena* instead of *C. Myxa* as the generic lectotype. Therefore, sects. *Cordia* and *Myxa* in their account are equivalent to sects. *Sebestenae* and *Cordia*, respectively, used in this treatment.

Taroda & Gibbs (1986a) have argued that *Cordia* should be retained *sensu lato* and that the infrageneric classification is better expressed by dividing *Cordia* into subgenera. They recognized three subgenera and three sections, of which sect. *Superbiflorae* Taroda is described as new, but because of their adoption of *C. Sebestena*, instead of *C. Myxa*, as the generic lectotype, they raised the wrong section to subg. *Cordia*. Therefore, subg. *Myxa* (Endl.) Taroda, which was published as a new subgenus rather than a new combination, should be recognized as subg. *Cordia*.

The morphological, palynological, and anatomical data strongly support the recognition of three major groups and three to five subgroups within *Cordia*. Whether these subdivisions are treated as genera, subgenera, sections, and/or subsections is only a matter of preference. Sections *Varronia* and *Sebestena* should perhaps be elevated to generic rank, but because *Cordia* is poorly represented in the southeastern United States and because it is beyond the scope of this flora to propose infrageneric adjustments to the classification of the genus, only sections are recognized here.

Section SEBESTENAE G. Don (*Sebestena* Boehmer in Ludwig, *Sebesten* Adanson, *Cordia* sect. *Sebestenoides* A. DC., *Cordia* sect. *Eucordia* Johnston) (shrubs or trees, inflorescence a lax, cymose panicle; calyx persistent, markedly accrescent, totally enclosing the drupe; corolla funnellform, reddish to orange or rarely white; pollen 3-colpate or 3-colporate, with striate-reticulate sexine) is a well-defined group that consists of about 16 species, all except two of which are indigenous to the New World. *Cordia subcordata* Lam. is a coastal species widespread in tropical Asia, East Africa from southern Somalia south to Mozambique, and the islands of the South Pacific and Indian Ocean, while *C. Suckertii* Chiov. is a bushland species restricted to central Somalia and easternmost Ethiopia (Warfa, 1988a).

Section SEBESTENAE is represented in the Southeast by two species, of which *C. Boissieri* A. DC. (*Lithocardium Boissieri* (A. DC.) Kuntze), Texas wild olive, $2n = 32$, is cultivated in Florida (Burch *et al.*; Miller, 1985a). The species is widely distributed in Mexico and southern Texas. It is easily distinguished by its white, funnellform corollas (3–4.5 cm long) and tomentose lower leaf surface. *Cordia Sebestena* L. (*C. speciosa* Salisb., *Sebesten Sebestena* (L.) Britton ex Small, Geiger tree, $2n = 32$, is an evergreen shrub or a small tree to 8 m tall, with scabrous, ovate leaves up to 22 cm long and 14 cm wide, funnellform, bright orange-red corollas to 6 cm long, and white, fleshy, accrescent



FIGURE 1. *Cordia*. a-m, *C. Sebestena*: a, leaf, $\times 1/4$; b, small inflorescence with most flowers failed, $\times 1\ 1/2$; c, flower, $\times 1$; d, e, opened corollas and gynoeceia of short- and long-styled flowers, respectively, $\times 1$; f, style and stigmas, $\times 3$; g, cross section of ovary at level of attachment of ovules, $\times 8$; h, fleshy, accrescent calyx enclosing fruit, $\times 3/4$; i, same as "h," but calyx partially sectioned to show drupe, $\times 3/4$; j, semidiagrammatic section of seeded drupe showing stone (hatched) with spongy inner tissue (stippled), aborted seed to left, and seed with embryo to right, $\times 2$; k, diagrammatic cross section of 2-seeded drupe showing two aborted and two mature seeds (convolution of cotyledons not shown), $\times 2$; l, embryo, $\times 4$; m, cross section of cotyledons at level of arrow in l, $\times 4$. n-p, *C. globosa*: n, leaf, $\times 1/2$; o, opened corolla, $\times 4$; p, mature fruit with calyx, $\times 4$.

calyx completely enclosing the white drupe and exceeding it by about a centimeter. It is apparently native to southernmost Florida, the Ba-

hamas, and the Greater Antilles (widely introduced elsewhere in the West Indies), and probably to the Caribbean coast of Central America in Mexico and that of Colombia and Venezuela (Johnston, 1935a). It is widely grown as an ornamental tree in the tropical and subtropical portions of the world. *Cordia Sebestena* grows on stabilized sand dunes and in hammocks in Dade, Lee, and Monroe counties, Florida, and occurs more abundantly on the Keys. Little (1978) indicated that the species is apparently introduced or naturalized in Florida, while Sargent and Tomlinson treated it as one of the native trees.

Proctor recognized plants of *Cordia Sebestena* in the Cayman Islands as the endemic var. *caymanensis* (Urban) Proctor. These are said to differ from var. *Sebestena* by a few overlapping characters that include smaller flowers and larger leaves that are not cordate at the base. Proctor also stated that the style is once forked if included and twice forked if exerted, but I have been unable to confirm this observation. As indicated above, branching of the style is the basic feature for distinguishing the subfamily Cordioideae from the Ehretioideae.

Section VARRONIA (P. Browne) Roemer & Schultes (*Varronia* P. Browne, *Cordia* subg. *Varronia* (P. Browne) Schecht. & Cham.; see Taroda & Gibbs (1986b) and Miller (1985a) for additional synonyms) (deciduous shrubs or rarely small trees; leaves serrate to dentate; inflorescences condensed cymose spikes, heads, or glomerules; calyx partially or totally enclosing the fruit; corolla white; pollen 3-porate, with a reticulate exine; fruits red drupes) includes about 60 species (Nowicke & Ridgway), all of which are indigenous to the New World. *Cordia curassavica* (Jacq.) Roemer & Schultes (Mexico, Central America, West Indies, northern South America), has become naturalized and widespread in tropical Africa and Asia (Nowicke *et al.*). The section, which ought to be recognized as an independent genus, is represented in the southeastern United States by a single indigenous species.

Cordia globosa (Jacq.) HBK. (*Varronia globosa* Jacq.; see Johnston (1949a, 1949b) for 13 additional synonyms) is widely distributed in the West Indies, Mexico, Central America, and northern South America. It is restricted in Florida to the coastal mainland of Dade and Monroe counties, but is more abundant on the Keys, particularly Key West (at least formerly) and Big Pine, Lignum Vitae, Summerland, and Windley's keys, where it grows on sand or limestone in thickets and hammocks. *Cordia globosa* is a weedy deciduous shrub to 4 m high, easily distinguished by its subterminal, capitate inflorescences (with sessile, distylous flowers), as well as white, tubular, obscurely lobed to undulate corollas to 1 cm long, red drupes with a bony, ovoid endocarp to ca. 5 mm long, and ovate to sub lanceolate leaves with serrate to somewhat crenate margins.

The nearest relative of *Cordia globosa* is *C. bullata* (L.) Roemer & Schultes, a shrub widely distributed in the Greater Antilles and from southern Mexico south to Nicaragua. Both Johnston (1949a) and Miller (1985a; 1988) distinguished the two species by characters that are basically continuous. *Cordia globosa* is said to have peduncles 0.5–2 cm

long and corollas 5–10 mm long, while *C. bullata* has peduncles 3–7 cm long and corollas 3–6 mm long. Furthermore, Miller (1988) indicated that the two species hybridize in Honduras and Nicaragua. Gaviria, on the other hand, reduced *C. globosa* to a subspecies, subsp. *humilis* (Jacq.) Gaviria, of *C. bullata*. He distinguished subsp. *bullata* as having heads to 1.5 cm in diameter, appendages of calyx teeth 1–2 mm long, and corollas 4–7 mm long. Subspecies *humilis* was said to have heads 1.5–2 cm in diameter, appendages 3–5(–6) mm long, and corollas 7–10 mm long. Johnston (1949a, b) recognized var. *globosa* (Lesser Antilles, Trinidad, Venezuela, and Brazil) by its larger leaves, with acute to acuminate apex and sharply serrate margins; and var. *humilis* (Jacq.) I. M. Johnston (Florida, Mexico, Central America, and Greater Antilles) by its smaller leaves with obtuse apex and teeth. Johnston (1949a) noted (p. 99) that these “differences are not always positive, especially in the Lesser Antilles.” Evidently, this complex is in need of a thorough study, and the differences used by Gaviria, Johnston (1949a, 1949b), and Miller (1985a, 1988) to distinguish species, subspecies, or varieties are all based on quantitative, continuous characters. In the absence of such a study, I am tentatively recognizing *C. globosa* and *C. bullata* as distinct species. Chapman reported the occurrence of *C. bullata* in Florida, but this record is almost certainly based on a misidentification of plants of *C. globosa*.

Section *CORDIA* (*Myxa* Endl., *Cordia* subg. *Myxa* (Endl.) Taroda, *Cordia* sections *Myxa* (Endl.) DC., *Micranthae* G. Don, *Pilicordia* DC., *Physoclada* DC.) (usually trees; inflorescences lax panicles; calyx caducous or persistent and not enclosing the fruit; corolla white, not marcescent; pollen 3-colporate, with spinulose sexine; drupes with leathery pericarp) is the largest in the genus, with more than 200 species. Section *Cordia*, as recognized here, corresponds fairly well to sect. *Myxa* of Taroda & Gibbs (1986a). It forms, together with sects. *Gerascanthus* (P. Browne) G. Don (ca. 25 species), *Superbiflorae* (6 species), and *Rhabdocalyx* A. DC. (3 species), a well-defined group characterized by 3-colporate pollen with spinulose sexine. This group, excluding sect. *Rhabdocalyx*, was treated by Taroda & Gibbs (1986a) as subg. *Myxa*. It consists of more than 240 species, none of which is indigenous to the southeastern United States. Burch, Ward, & Hall listed six species as cultivated in Florida. These include *Cordia alliodora* (Ruíz & Pavón) Oken (Mexico, Central America, tropical South America) of sect. *Gerascanthus*, and *C. africana* Lam. (tropical Africa, southern Arabia), *C. dentata* Poiré (Mexico, Central America, West Indies, Colombia, Venezuela), *C. lutea* Lam. (Galapagos Islands, Ecuador, Peru), *C. laevigata* Lam. (as *C. nitida* Vahl) (Greater Antilles, Cayman Islands, Virgin Islands), and *C. Myxa* (as *C. obliqua* Willd.) of sect. *Cordia*. The natural range of the last species is tropical Asia (Warfa, 1988a); it is widely cultivated in various tropical, subtropical, and warm regions of the world.

The breeding systems in *Cordia* are diversified, and distyly, which is widespread throughout all sections of the genus, is believed to be primitive (Johnston, 1950; Opler *et al.*; Miller, 1985a, 1988). Heterostyly is

often associated with self-incompatibility and dimorphism in the size of pollen grains; pollen grains of the short-styled plants are significantly larger. Dioecism and homostyly have each evolved from distyly independently in the various sections of the genus. Homostyly has evolved at least three times (sects. *Cordia*, *Gerascanthus*, and *Varronia*) and dioecism at least twice (sects. *Cordia* and *Varronia*) (Johnston, 1940; Gibbs & Taroda; Miller, 1985a; Opler *et al.*).

The evolution of homostyly from distyly in *Cordia* involved the breakdown of self-incompatibility to self-compatibility and the loss of the long-styled morph. In *C. alliodora*, which is the most widespread species in the genus (Miller, 1988), both homostylous and short-styled forms are found (Gibbs & Taroda), and the majority of plants is self-incompatible (Mendoza, in Opler *et al.*). In *C. trichotoma* (Vell.) Arráb. ex Steudel, a very close relative of *C. alliodora*, long-styled, homostylous, and short-styled forms are found (Gibbs & Taroda).

The flowers of *Cordia Sebestena* are distylous, and the differences in the relative positions of anthers and stigmas in the two flower forms may be correlated with bimodal variation in corolla size. The stamens are included and the styles are exerted in the smaller-flowered form, while the reverse is true in the larger-flowered one. Although these flower forms resemble those of heterostylous species, the basic difference is the anther position that is caused by heterocorollary, where the difference in corolla size affects the height of anthers. The stigmas are borne at the same height in both flower forms, but the anthers are raised above them in the large-flowered form (Tomlinson; Miller, 1985a). The species apparently flowers throughout most of the year, but fruiting seems more abundant in midsummer in Florida (Tomlinson).

The evolution of dioecism from distyly has been thoroughly reviewed in various families of flowering plants (Ganders; Vuilleumier). *Cordia* follows the same pattern in that the staminate plants have evolved by the reduction of the style in the short-styled morphs, while the carpellate plants originated by the abortion of the stamens in the long-styled forms (Opler *et al.*). Dioecism is widespread in *Cordia*, and Gaviria, Johnston (1940), and Miller (1988) have reported it in many species. The development of dioecism, however, varies within certain species. For example, in *C. inermis* (Miller) I. M. Johnston, a weedy plant of Central America, the carpellate flowers have nonfunctional anthers and are 100 percent male sterile, whereas the staminate ones have reduced gynoecea that have retained a slight fertility because they occasionally produce fruits (Miller, 1988; Opler *et al.*). According to Miller (1985a), the species is subdioecious, and (p. 101) "perhaps represents an intermediate stage in the evolution of dioecy from distyly."

Other types of reproductive systems have been reported for *Cordia*, including parthenocarpy in *C. dichotoma* Forster f. (Johshi); polygamy in *C. Myxa* (Hutchinson), *C. sinensis* Lam. and *C. monoica* Roxb. (noted as "trioecious") (Warfa, 1988a); and suspected agamospermy in *C. crenata* Del. subsp. *crenata* and *C. obovata* Balf. f. (Warfa, 1988a).

However, the reports of agamospermy and parthenocarpy need to be verified.

The flowers of *Cordia* are visited by a wide range of pollinators, including a very large number of insects that belong to numerous families, particularly of the orders Coleoptera, Diptera, Hymenoptera and Lepidoptera (Opler *et al.*). Percival observed in Jamaica that the flowers of *C. Sebestena* are pollinated by the hummingbirds *Trochilus polytmus* and *Coerebla flaveola*, whereas those of *C. Gerascanthus* L. are pollinated by the latter and the hummingbird *Mellisuga humilis*, which also pollinates *C. globosa*. On St. John, U.S. Virgin Islands, nearly 56 percent of the flowers of *C. Sebestena* are pollinated by the hummingbirds *Eulampis holosericeus* and *Orthorhynchus cristatus* (Askin *et al.*). The bright reddish-orange corolla with long tube, the abundant nectar, and the clustering of flowers of *C. Sebestena* are all adaptations to hummingbird pollination. Miller (1985a) indicated that the flowers of *C. Sebestena* are visited by orioles. Warfa (1988a) observed that the flowers of *C. Suckertii* were pollinated in Somalia by the sunbirds *Anthreptes orientalis* and *Nectarinia amethystina*. Bat pollination of *Cordia* in Mexico has been reported by Alvarez & Quintero.

Chromosome numbers have been reported for only about 23 species (ca. seven percent) of *Cordia*. The chromosome data are summarized in Miller (1985a) and Gaviria, and additional counts are given in Coleman and Wiggins (1971). The scant data do not give any support to the infrageneric classification of *Cordia*. All except three of the species surveyed are polyploids based on seven, eight, or nine. The diploid *C. Pringlei* Robinson has $2n = 14$ (Miller, 1985a); *C. bullata* has $2n = 16$ (Gaviria), and *C. curassavica* (Jacq.) Roemer & Schultes (as *C. verbenacea* DC.) has $2n = 18$ (Coleman). These diploid species all belong to sect. *Varronia*, but as indicated above this section should perhaps be recognized as a distinct genus, and many more chromosome counts are needed before any meaningful conclusions can be reached.

On the basis of available data on chromosome numbers and breeding systems, Opler and colleagues postulated that the ancestors or the most primitive members of *Cordia* were heterostylous, had a haploid number of eight, and were pollinated by Lepidoptera. They suggested that polyploidy and dioecism each evolved independently several times within the genus, and that the shift to dioecism was associated with the aneuploid reduction of chromosome number from $n = 16$ to $n = 14$. In other species the shift from heterostyly to homostyly was accompanied by the partial breakdown of self-incompatibility and aneuploidy. Another trend they observed is the change in size and in other aspects of flowers in connection with the attraction of smaller pollinators, such as bees and flies, or larger ones, such as birds and bats.

Interspecific hybridization has been well documented only among certain species of sect. *Varronia* (Miller, 1985a, b, 1988). No inter-sectional hybrids have been reported. Members of sect. *Varronia* that have overlapping ranges are usually reproductively isolated by habitat

preference, and hybridization takes place primarily in disturbed habitats within areas of sympatry. Interspecific hybrids between *Cordia bullata* and the closely related *C. globosa* produce some viable pollen, and backcrossing and "introgression" occur in Honduras and Nicaragua (Miller, 1985b, 1988). In contrast, the interspecific hybrids of *C. bullata* and the remotely related *C. curassavica* are sterile, but are known to persist and spread by the production of rhizomes.

Cordia is poorly studied chemically, and the very scant data do not help in the infrageneric classification of the genus. Moir & Thomson studied the occurrence and chemistry of some six terpenoid benzoquinones among 16 species and found that the distributional profiles of these compounds might have some chemotaxonomic value. The report of cyanolipids in a species of *Cordia* as unique to the Boraginaceae (Seigler *et al.*) was shown by Seigler to be based on a misidentified plant of *Allophyllus* of the Sapindaceae.

Among the anatomical peculiarities of *Cordia* is the occurrence of crystalline cellular inclusions. Gottwald (1983) has shown that the wood of various species contains crystal sand and/or prismatic crystals. The sand is an aggregation of numerous tiny, pyramidal crystals and has been found alone in the wood of members of sect. *Varronia*, while prismatic crystals are found in members of sect. *Gerascanthus*. A mixture of both types was found in the remaining sections of *Cordia*. Taroda & Gibbs (1986a) found that these anatomical data support their infrageneric classification of *Cordia*.

In some species of *Cordia*, in which the pericarp is woody, Roth observed that both the epidermis and hypodermis have small, thick-walled cells and that almost the entire fruit wall consists of cartilaginous collenchyma, the cells of which have irregular shapes because of uneven wall thickening and enlarged pits. The inner part of the pericarp contains large tracheids with spiral wall thickenings.

Various sections of *Cordia* have diverse fruit types that are adapted to different dispersal mechanisms. The unit of dispersal in *Cordia* is the whole fruit, which always has a single stone.

The fruits of sect. *Varronia* are fleshy, usually bright red drupes that rarely exceed 5 mm in length and have only the lower half subtended by the persistent calyx. These fruits are eaten by birds such as parrots (*Amazona* spp.) and parakeets of the genera *Aratinga* and *Brotogeris* (Opler *et al.*). Therefore, it is very likely that the fruits of plants in this section are dispersed for relatively long distances. Single collections of various West Indian species of sect. *Varronia* are known from Florida (J. S. Miller, personal comm.). These may well represent recent dispersal by birds of self-incompatible *Cordia* species.

The fruits of sect. *Cordia* are much larger than those of sect. *Varronia* and are subtended at the base by a cup- or saucer-shaped persistent calyx. They are white, yellow, orange, or red and have a mucilaginous, usually sweet, well-developed mesocarp. These are usually dispersed in the New World by arboreal mammals such as the howler monkey and coatimundi (Opler *et al.*) and by various other monkeys in Africa

(Warfa, 1988a). The smaller fruits of some species are usually bird dispersed.

All species of sect. *Gerascanthus* have persistent marcescent corollas that enclose the lower part of the usually large, dry, thin- and fibrous-walled fruit. These fruits, which are unique to this section, are capped by the persistent base of the style. They are dispersed by wind for short distances, the persistent corolla acting as a parachute. As indicated by Miller (1985a), however, the fruits of sect. *Gerascanthus* are fairly heavy and effective wind dispersal is unlikely. Much of the fruit dispersal in this section, therefore, may take place by rain wash or by being blown along the ground by wind.

Johnston (1951a) pointed out that the fruits of *Cordia subcordata* are well adapted to dispersal by water because of their woody endocarp, corky mesocarp, and fleshy, persistent calyx. They float on water and tolerate salinity for a prolonged period. These adaptations account for the wide distribution of the species along the coasts of the Indian Ocean. Warfa (1988a) suggested that fruits of the closely related *C. Suckertii* are perhaps dispersed by ground squirrels.

A number of species of *Cordia* are grown as ornamentals, and *C. Sebestena* is widely cultivated throughout the warm and tropical parts of the world for its attractive, large, bright orange-red (to yellow) flowers, whereas *C. dentata* is grown in Florida and Central America for its showy, relatively large, yellow flowers.

The timber of *Cordia alliodora*, *C. Gerascanthus* L., *C. Sebestena*, and *C. subcordata* is often pleasant smelling and takes an excellent finish. It is used locally for making furniture, musical instruments, and boats (I. H. Burkill).

The fruits of members of section *Cordia* are edible, and *C. Myxa* is perhaps the most widely used of all species. The fresh fruits, which were formerly known as sebesten or sebesten plum, are sweet, pleasant tasting, thirst quenching, mildly laxative, and slightly astringent. The dried fruits are employed as a remedy for chest ailments and coughs. The green fruits are eaten as a vegetable, pickled, or used as a source of temporary glue. The bark of *C. Myxa* is used to prepare a decoction said to be good for dyspepsia, dysentery, and ulcers (I. H. Burkill).

The leaves of several species are eaten by cattle, and those of *Cordia Sebestena* are said to be used as a sandpaper to polish tortoise shell (Proctor). The West Indian *C. curassavica* has become a noxious weed in parts of Malaysia following its introduction in 1954.

REFERENCES:

- Under family references see ADAMS; ALAIN; AL-NOWAIHI *et al.*; ARISTEGUI-ETA; AYENSU; BAILEY; BAILEY *et al.*; BAILLON; BAKER & WRIGHT; BARAJAS MORALES (1981, 1983); BATE-SMITH; BELL & TAYLOR; BENTHAM & HOOKER; BHATTACHARYA; BOLKHOVSKIKH *et al.*; BRITTON; BRITTON & BROWN; BULL *et al.*; H. M. BURKILL; I. H. BURKILL; DE CANDOLLE; CHAPMAN; CORRELL & CORRELL (1972, 1982); CORRELL & JOHNSTON; DARWIN; ELIAS; GANDERS; GIBSON; GOLDBLATT (1981, 1984, 1985, 1988); GRAF; GUPTA; HARRAR & HARRAR; HEDRICK;

- HEINE; HOWARD; JOHNSTON (1935a, b, 1936, 1937, 1948, 1949, 1951 a, 1952, 1956); JOHNSTON *et al.*; KNUTH; LAKELA & CRAIGHEAD; LITTLE (1978, 1979); LONG & LAKELA; LUBBOCK; MACBRIDE (1960); MARTICORENA; MARTINS; R. B. MILLER (1989); R. J. MOORE (1973, 1977); MORTON; NASH & MORENO; NEUBAUER; NOWICKE; NOWICKE & MILLER (1987); PATEL *et al.*; PERRY; PROCTOR; QUISUMBING; RECORD & HESS (1941); RECORD & MELL; RIDLEY; ROTH (1973); SARGENT; SATYAVATHI & NARAYANA; SMALL (1903, 1913, 1933); L. B. SMITH; STANDLEY; STEARN; SYNGE; TATON; UPHOF; VUILLEUMIER; WARD & FANTZ; WIGGINS (1971); WILLIS; and WUNDERLIN.
- AGNIHOTRI, V. K., S. D. SRIVASTAVA, S. K. SRIVASTAVA, S. PITRE, & K. RUSIA. Constituents from the seeds of *Cordia obliqua* as potential anti-inflammatory agents. *Indian Jour. Pharm. Sci.* **49**: 66-69. 1987.*
- AGOSTINI, G. A new Venezuelan species of *Cordia* sect. *Gerascanthus* (Boraginaceae). *Brittonia* **25**: 174-176. 1973. [*C. Thaisiana*, sp. nov.; key to the species of sect. *Gerascanthus* in northern South America.]
- ALMEIDA, D. G. DE. Notes on a *Cordia* wood from eastern Brazil. *Trop. Woods* **89**: 48-52. 1947. [Wood anatomy of six species.]
- ALVAREZ, T., & L. G. QUINTERO. Análisis polínico del contenido gástrico del murciélagos Glossophaginae de México. *Anal. Esc. Nac. Cienc. Biol. México* **18**: 137-165. 1970. [Bat pollination in *Cordia*, 165.]
- ASHRAF, M., S. A. KHAN, & M. K. BHATTY. Fatty acids of indigenous resources for possible industrial applications. Part III.—Investigation of some species of Boraginaceae family. *Pakistan Jour. Sci. Indus. Res.* **14**: 399. 1971. [*C. Myra*, *C. obliqua*, *C. Rothii*.]
- ASKINS, R. A., K. M. ERCOLINO, & J. D. WALLER. Flower destruction and nectar depletion by avian nectar robbers on a tropical tree, *Cordia Sebestena*. *Jour. Field Ornithol.* **58**: 345-349. 1987. [Pollination by two species of hummingbirds, and nectar-robbing by three nonpollinating birds.]
- BAILEY, I. W. Notes on neotropical ant-plants. III. *Cordia nodosa* Lam. *Bot. Gaz.* **77**: 32-49. pls. 6, 7. 1924. [Anatomy of ant domatia in three species of *Cordia*.]
- BHATTY, M. K., D. H. SHAH, M. A. SAEED, & NASIRUDDIN. Studies of a carbohydrate-containing polymer from *Cordia Myra*. *Pakistan Jour. Sci. Indus. Res.* **21**: 162, 163. 1978.
- BISEN, S. S., & B. SHARMA. An unusual vessel perforation plate in *Cordia Myra* L. (Boraginaceae). *IAWA Bull.* **II**. **6**: 163, 164. 1985. [Reticulate perforation plates with minute druses and acicular and cubical crystals.]
- BRADE, A. C. Os generos *Cordia* e *Tournefortia*. *Bol. Mus. Nac. Rio de Janeiro* **8**: 13-47. 2 pls. 1932. [Fifty species of *Cordia* in Brazil; keys to sections and species, enumerations, synonymy, illustrations.]
- BRITTON, N. L. North American trees. x + 894. New York. 1908. [*Cordia*, 817-819; *C. Boissieri*, *C. Sebestena*; first typification of *Cordia*.]
- & P. WILSON. Scientific survey of Porto Rico and the Virgin Islands. Vol. 6. 158 pp. 1925. [*Cordia* divided into the segregates *Cerdana*, *Calyptracordia*, *Sebesten*, *Cordia*, and *Varronia*; *Cordia glabra* as type species; 123-128.]
- BURCH, D., D. B. WARD, & D. W. HALL. Checklist of the woody cultivated plants of Florida. 80 pp. Extension Sale Publ. SP-33. Inst. Food Agr. Sci., Univ. Florida, Gainesville. 1988. [*C. africana*, *C. alliodora*, *C. Boissieri*, *C. dentata*, *C. globosa*, *C. lutea*, *C. nitida*, *C. obliqua*, *C. Sebestena*; 24, 25.]
- CHEN, T. K., D. C. ALES, N. C. BAENZIGER, & D. F. WIEMER. Ant-repellent triterpenoids from *Cordia alliodora*. *Jour. Org. Chem.* **48**: 3525-3531. 1983. [Six leaf-triterpenoids are ant repellent.]
- CHUDNOFF, M. Tropical timbers of the world. U.S. Dep. Agr. Handb. 607. Washington, D.C. 1984. [*Cordia*, 55-57, 205, 323, 431.]

- COLEMAN, J. R. Chromosome numbers of angiosperms collected in the state of São Paulo. *Rev. Brasil. Genét.* **5**: 533-549. 1982. [*C. verbenacea*, $n = 9$.]
- CORNER, E. J. H. Wayside trees of Malaya. ed. 3. Vol. 1. xxii + 476 pp. + 138 pls. Kuala Lumpur. 1988. [*Cordia*, 197-199, pl. 41.]
- DOMÍNGUEZ, X. A., S. ESCARRIA, & D. BUTRUILLE. Dimethyl-3,4'-kaempferol de *Cordia Boissieri*. *Phytochemistry* **12**: 724, 725. 1973. [A related paper in *Ibid.* 2296.]
- FARR, E. R., J. A. LEUSSINK, & F. A. STAFLEU. Index nominum genericorum (plantarum). Vol. 1. *Regnum Veg.* **100**. xxvi + 630 pp. 1979. [*Cordia*, 421.]
- FATHIMA, T. Sporogenesis and the development of gametophytes in *Cordia alba* L. *Curr. Sci. Bangalore* **35**: 73, 74. 1965. *
- FRIESEN, B. C. Les caractères essentiels de la famille des Sebestenaceae et revision du genre *Varronia*. *Bull. Soc. Bot. Genève* **II**. **24**: 117-201. 1933. [*Cordia* abandoned and its component species segregated into ten genera.]
- GAVIRIA, J. Die Gattung *Cordia* in Venezuela. *Mitt. Bot. Staatssamml. München* **23**: 1-279. 1987. [Forty-two species; morphology; palynology; cytology; descriptions, distributions, illustrations, maps, key.]
- GIBBS, P. E., & N. TARODA. Heterostyly in the *Cordia alliodora*-*C. trichotoma* complex in Brazil. *Revista Brasil. Bot.* **6**: 1-10. 1983. [Flowers of *C. alliodora* range from short-styled to homostylous, while those of *C. trichotoma* are long-styled, short-styled, and homostylous.]
- GONZÁLEZ, M. E., L. LLACH, & G. GONZÁLEZ. Maderas latinoamericanas. VII. Características anatómicas, propiedades fisicomecánicas, de secado, y tratabilidad de la madera juvenil de *Cordia alliodora* (Ruíz & Pav.) Oken. (English summary.) *Turrialba* **21**: 350-356. 1971.
- GOTTWALD, H. 'Louro Preto'—found to be the first silica-bearing *Cordia* (*Cordia glabrata*, Boraginaceae). *IAWA Bull.* **II**. **1**: 55-58. 1980. [First report of silica grains in the Boraginaceae.]
- . Wood anatomical studies of Boraginaceae (s. l.). I. Cordioideae. *Ibid.* **4**: 161-177. 1983. [*Auzemma*, *Cordia*, *Patagonula*; genera distinguishable anatomically; wood anatomy supports the placement of 95 species of *Cordia* in eight sections.]
- HEINE, H. A propos de la nomenclature d'un sébestier de l'ancien monde. *Adansonia* **II**. **8**: 181-187. 1968. [*C. sinensis*; see MEIKLE.]
- HITCHCOCK, A. S., & M. L. GREEN. Standard-species of Linnean genera of Phanerogamae (1753-1754). Pp. 111-199 in *Internatl. Bot. Congress, Cambridge, England, 1930. Nomenclature. Proposals by British botanists.* London. 1929. [*Cordia*, 133.]
- HOYOS, J. Flora tropical ornamental. 430 pp. Caracas. 1978. [*C. alliodora*, *C. collococca*, *C. Sebestena*, 320-322; brief notes (in Spanish), distribution, description, uses; colored photographs.]
- HUTCHINSON, J. *Cordia Myxa* and allied species. *Bull. Misc. Inf. Kew* **1918**: 217-222. 1918. [*C. crenata*, *C. Myxa*, *C. obliqua*; key, distributions, illustrations.]
- IFZAL, S. M., & A. QURESHI. Studies on *Cordia Myxa*. Part I. The monosaccharide and polysaccharide components of fruits of *Cordia Myxa*. *Pakistan Jour. Indus. Res.* **19**: 64, 65. 1976.
- JANKIEWICZ, L. S., M. T. C. LEÓN, & V. M. MARINEZ-ALBORES. Cupapé (*Cordia dodecandra* DC., Boraginaceae) a fruit tree in the process of domestication in Mexico. *Acta Soc. Bot. Pol.* **55**: 115-127. 1986.
- JOHNSON, P., & R. MORALES. A review of *Cordia alliodora* (Ruíz & Pav.) Oken. (Spanish summary.) *Turrialba* **22**: 210-220. 1972. [Nomenclature, description, distribution, agriculture, pests and diseases, wood anatomy and properties.]
- JOHNSTON, I. M. Studies in the Boraginaceae,—VIII. I. Observations on the species of *Cordia* and *Tournefortia* known from Brazil, Paraguay, Uruguay and Argentina. *Contr. Gray Herb.* **92**: 1-89. 1930. [*Cordia*, 5-26; typification, sectional classification, keys, descriptions, distributions.]

- . Studies in the Boraginaceae, XV. Notes on some Mexican and Central American species of *Cordia*. Jour. Arnold Arb. **21**: 336–355. 1940. [Dioecism, heterostyly; key and treatment of 20 species of sect. *Pilicordia*.]
- . Studies in the Boraginaceae, XVII. A. *Cordia* sect. *Varronia* in Mexico and Central America. *Ibid.* **30**: 85–110. 1949. [Sixteen species; nomenclature, distribution, notes, key.]
- . Studies in the Boraginaceae, XIX. *Ibid.* **31**: 172–187. 1950. [*Antrophora*, gen. nov.; new species of *Cordia*; *Cordia* sect. *Gerascanthus* in Mexico and Central America.]
- JOSHI, B. M. Structure and development of seed coat and pericarp in parthenocarpic fruits of *Cordia dichotoma*. Geobios India **4**: 201–220. 1977.*
- KHALEEL, T. F. Embryology of *Cordia*. Bot. Gaz. **136**: 380–387. 1975. [*C. alba*, *C. obliqua*; micro- and megasporogenesis.]
- . Embryology of *Cordia Sebestena* (Boraginaceae). Pl. Syst. Evol. **139**: 303–312. 1982. [Mega- and microsporogenesis, development of gametophytes, systematic position of the Cordioideae.]
- KILLIP, E. P. New species of *Cordia* and *Tournefortia* from northwestern South America. Jour. Washington Acad. Sci. **17**: 327–335. 1927. [*Cordia* (10 spp.) and *Tournefortia* (7 spp.).]
- LEÓN GÓMEZ, C., & J. B. MORALES. Variación de la estructura de la madera en *Cordia elaeagnoides* DC. (English summary.) Biotica **12**: 121–129. [Comparative anatomy of wood at different heights in plants; juvenile wood restricted to the core region of stem.]
- LITTLE, E. L., JR., R. O. WOODBURY, & F. H. WADSWORTH. Trees of Puerto Rico and the Virgin Islands. Vol. 2. U.S. Dep. Agr., Agr. Handb. 449. xiv + 1024 pp. 1974. [*Cordia*, 840–849.]
- LLOYD, D. G. Evolution towards dioecy in heterostylous populations. Pl. Syst. Evol. **131**: 71–80. 1979. [Five species of *Cordia*; see OPLER *et al.*]
- MEIKLE, R. D. The nomenclature of *Cordia Gharaf*. Israel Jour. Bot. **18**: 141–143. 1969. [A supplementary note in *Ibid.* **20**: 21–23. 1971; *C. sinensis* the correct name for the species widely known as *C. Gharaf*; see HEINE.]
- MEZ, C. Morphologische und anatomische Studien über die Gruppe der Cordieae. Bot. Jahrb. **12**: 526–528. pls. 4, 5. 1890. [Twelve sections of *Cordia*; trichome types, cystoliths; new taxa.]
- MIERS, J. On the Auxemmeae, a new tribe of the Cordiaceae. Trans. Linn. Soc. London Bot. II. **1**: 23–36. pls. 5–8. 1875. [*Auxemma*, *Hymenesthes*, *Paradigma*, and *Plethostephia* segregated as new genera from *Cordia*; *Patagonula*, *Sacellium*.]
- MILLER, J. S. Systematics of the genus *Cordia* (Boraginaceae) in Mexico and Central America. ix + 686 pp. Unpubl. Ph.D. dissertation. St. Louis University, St. Louis, Missouri. 1985a.
- . Hybridization in *Cordia* section *Varronia* (Boraginaceae). (Abstract.) Am. Jour. Bot. **72**: 693. 1985b. [Hybrids between *C. bullata* and each of *C. curasavica* and *C. globosa*.]
- . *Cordia Mcvaughii*, a new species of Boraginaceae from western Mexico. Syst. Bot. **11**: 579–582. 1986. [Key to the Mexican species of sect. *Cerdanae*; heterostyly.]
- . Two new species of *Cordia* (Boraginaceae) from Central America. Ann. Missouri Bot. Gard. **74**: 670–673. 1987. [*C. Liesneri* and *C. Cardenasiana*, spp. nov.]
- . A revised treatment of Boraginaceae for Panama. *Ibid.* **75**: 456–521. 1988. [*Cordia*, 463–497; 27 species, including five described as new.]
- . Notes on the *Cordia panamensis* complex (Boraginaceae) and a new species from Colombia. *Ibid.* **76**: 593–595. 1989. [*C. Gentryi*, sp. nov.; key to ten species.]

- & J. W. NOWICKE. Sectional placement of some problematic *Cordia* species (Boraginaceae). *Syst. Bot.* **14**: 271–280. 1989. [Pollen morphology and sectional classification, sectional disposition of 24 species.]
- MOIR, M., & R. H. THOMSON. Naturally occurring quinones. Part XXII. Terpenoid quinones in *Cordia* spp. *Jour. Chem. Soc. Perkin Transact.* **1973**: 1352–1357. 1973. [Distribution and characterization of six terpenoid benzoquinones in 16 species of *Cordia*.]
- , B. M. HAUSEN, & M. H. SIMATUPANG. Cordiachromes: a new group of terpenoid quinones from *Cordia* spp. *Jour. Chem. Soc. Chem. Commun.* **1972**: 363, 364. 1972. [*C. Millenii*; timber contains six benzoquinones.]
- MONCADA, M., & P. HERRERA OLIVER. La palinología del género *Cordia* (Angiospermae: Boraginaceae) en Cuba. *Acta Bot. Cubana* **58**. 10 pp. 1988. [Twenty-three species, including *C. globosa* and *C. Sebestena*.]
- NETO, G. G., & N. M. ASAKAWA. Estudio de mirmecodomaáceos em algumas espécies de Boraginaceae, Chrysobalanaceae, Melastomataceae e Rubiaceae. (English summary.) *Acta Amazon.* **8**: 45–49. 1978. [Ant domatia on *C. nodosa*.]
- NOWICKE, J. W., J. S. MILLER, & J. L. BITTNER. Pollen morphology of *Cordia Sebestena* and *C. subcordata* (Boraginaceae). *Jour. Palyn.* **23/24**: 59–64. 1987/1988. [Pollen morphology and sectional classification of *Cordia*; heterostyly.]
- & J. E. RIDGWAY. Pollen studies in the genus *Cordia* (Boraginaceae). *Am. Jour. Bot.* **60**: 584–591. 1973. [Pollen of 40 species; correlation of pollen characteristics with inflorescence, flower and fruit morphology support raising sect. *Varronia* and *C. Sebestena* with its relatives to two genera; lectotypification of *Cordia*.]
- OPLER, P. A., H. G. BAKER, & G. W. FRANKIE. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* **7**: 234–247. 1975. [Eight species; breeding systems, pollination biology, dispersal.]
- & K. S. BAWA. Sex ratios in tropical forest trees. *Evolution* **32**: 812–821. 1978. [*C. collococca* and *C. panamensis*; higher ratios of staminate to carpellate plants.]
- PALACIOS-CHÁVEZ, R. Observaciones en el pólen de plantas con probable polinización quiropterófila. (English summary.) *Anal. Esc. Nac. Cienc. Biol. México* **21**: 115–143. 1974. [*C. igualensis*, *C. oaxacana*, pollen.]
- & D. L. QUIROZ-GARCÍA. Catálogo palinológico para la flora de Veracruz. No. 22. Familia Boraginaceae. Género *Cordia*. (English summary.) *Biotica* **10**: 71–113. 1985. [Seventeen species; light and scanning-electron microscopy, 30 plates.]
- PERCIVAL, M. Floral ecology of coastal scrub in Southeast Jamaica. *Biotropica* **6**: 104–129. 1974. [*Cordia*; heterostyly, phenology, pollinators.]
- RAO, B. H., & P. S. P. RAO. Sporogenesis and genesis of gametes in *Cordia Sebestena* L. *Acta Bot. Indica* **12**: 69–76. 1984.
- RODRÍGUEZ, R., O. MATTHEI, & M. QUEZADA. Flora arbórea de Chile. 408 pp. Concepción, Chile. 1983. [*C. decandra*, 104–106.]
- ROTH, I. Stratification of a tropical forest as seen in dispersal types. In: H. LIETH & H. A. MOONEY, eds., *Tasks for vegetation science*. Vol. 17. x + 324 pp. Dordrecht, Boston, and Lancaster. 1987. [*Cordia*, 60, 61; dispersal, pericarp anatomy.]
- SALAS, G. DE LAS, & J. VALENCIA. Notas sobre la reforestación con *Cordia alliodora* (Ruíz & Pav.) Oken en dos zonas tropicales de Bajura; Tumaco y Carare-Opón, Colombia. (English summary.) *Corpor. Nac. Investig. Fomento Forest. Ser. Téc.* **10**. 34 pp. 1979.
- SARGENT, C. S. The silva of North America. Vol. 6. vii + 124 pp. pls. 252–300. Boston and New York. 1894. [*Cordia*, 67–74, pls. 281–284; *C. Sebestena*, *C. Boissieri*.]

- SASTRI, B. N., ed. The wealth of India. Vol. 2. *Frontisp.* + xx + 427 pp. + 17 pls. Delhi. 1950. [*Cordia*, 346, 347.]
- SCURFIELD, G., A. J. MICHELL, & S. R. SILVA. Crystals in woody stems. *Bot. Jour. Linn. Soc.* **66**: 277–289. 7 pls. 1973. [*C. Sebestena* contains “crystal sand” in the vertical parenchyma of wood.]
- SEIGLER, D. S. Cyanolipids in *Cordia verbenacea*—a correction. *Biochem. Syst. Ecol.* **4**: 235, 236. 1976. [*C. Boissieri*, *C. dodecandra*, *C. subpubescens*, and *C. verbenacea* contain no cyanolipids; report of SEIGLER *et al.* was based on plant misidentification.]
- , K. L. MIKOLAJCZAK, C. R. SMITH, JR., I. A. WOLFF, & R. B. BATES. Structure and reactions of a cyanogenetic lipid from *Cordia verbenacea* DC. seed oil. *Chem. Phys. Lipids* **4**: 147–161. 1970. [See SEIGLER for correction.]
- SERTIÉ, J. A. A., A. C. BASILE, S. PANIZZA, A. K. MATIDA, & R. ZELNIK. Pharmacological assay of *Cordia verbenacea*; Part I. Anti-inflammatory activity and toxicity of the crude extract of the leaves. *Pl. Med.* **54**: 7–10. 1988. [Inhibition of edema and reduction of granuloma formation in rats.]
- SHAH, J. J., & R. JACOB. Slime bodies in the companion cells of *Cordia Sebestena* L. *Curr. Sci. Bangalore* **36**: 301, 302. 1967.*
- SIMMONDS, F. J. Biological control of *Cordia curassavica* (Boraginaceae) in Malaysia. *Entomophaga* **25**: 363, 364. 1980. [Introduction of the beetle *Metrogaleruca* and the wasp *Eurytoma* to control *C. curassavica*.]
- TARODA, N. Taxonomic studies on Brazilian species of *Cordia* L. (Boraginaceae). 231 pp. Unpubl. Ph.D. dissertation. Univ. St. Andrews, Scotland. 1984.*
- & P. GIBBS. Studies on the genus *Cordia* L. (Boraginaceae) in Brazil. 1. A new infrageneric classification and conspectus. *Rev. Brasil. Bot.* **9**: 31–42. 1986a. [Taxonomic history, palynology, recognition of three subgenera.]
- & ———. A revision of the Brazilian species of *Cordia* subgenus *Varronia* (Boraginaceae). *Notes Bot. Gard. Edinburgh* **44**: 105–140. 1986b. [Thirty species; key, descriptions, illustrations; *C. globosa* is distylous.]
- & ———. Studies on the genus *Cordia* L. (Boraginaceae) in Brazil. 2. An outline taxonomic revision of subgenus *Myra* Taroda. *Hoehnea* **14**: 31–52. 1987. [Thirty-five species in three sections; keys, synonymy, citations.]
- TIWARI, K. P., & S. S. D. SRIVASTAVA. Chemical investigation of the stem bark of *Cordia obliqua*. *Pl. Med.* **36**: 191, 192. 1979.
- TOMLINSON, P. B. The biology of trees native to tropical Florida. [ix] + 480 pp. Allston, Massachusetts. 1980. [*Cordia*, 112–114; largely *C. Sebestena*, including a detailed illustration (but some details inaccurate); *C. globosa* mentioned.]
- TOWNSEND, C. C. Ehretiaceae. In: C. C. TOWNSEND & E. GUEST, eds., *Fl. Iraq* **4**: 644–647. 1980. [*Cordia*, *Ehretia*.]
- UHLARZ, H., & F. WEBERLING. Ontogenetische Untersuchungen an *Cordia verbenacea* DC. (Boraginaceae), ein Beitrag zur Kenntnis der Syndesmen. (English summary.) *Ber. Deutsch. Bot. Ges.* **90**: 127–134. 1977.
- UNG, S. H., A. YUNUS, & W. H. CHIN. Biological control of *Cordia curassavica* (Jacq.) R. & S. in Malaysia by *Schematiza cordiae* Barb. (Coleop.: Galerucidae). *Malay. Agr. Jour.* **52**: 154–165. colored pl. 1979.
- VERDCOURT, B. A new species of *Cordia* (Boraginaceae) from East Africa. *Bol. Soc. Brot.* **II** **53**: 103–111. 1980. [*C. Faulknerae*, sp. nov.]
- WARFA, A. M. *Cordia* (Boraginaceae) in NE tropical Africa and tropical Arabia. *Acta Univ. Uppsala* **174**. 78 pp. 1988a. [Sixteen species; morphology, nomenclature, palynology, taxonomy; key, maps.]
- . *Cordia africana* Lam. (Boraginaceae), the correct name for Bruce's “Wanzey.” *Taxon* **37**: 961–963. 1988b. [*C. abyssinica* reduced to synonymy of *C. africana*.]
- . The identity and distribution of *Cordia obtusa* (Boraginaceae). *Nordic Jour. Bot.* **8**: 489–491. 1989a. [A rare African species.]

- . Taxonomy and distribution of *Cordia crenata* (Boraginaceae). *Ibid.* 613-618. 1989b. [Two subspecies recognized; illustrations, map.]
- . A new species of *Cordia* (Boraginaceae) from Kenya. *Ibid.* 9: 251, 252. 1989c. [*C. longipetiolata* is endemic to Kenya.]
- WIGGINS, I. L. Boraginaceae. Pp. 277-296 in I. L. WIGGINS & D. M. PORTER, Flora of the Galápagos Islands. Stanford. 1971. [*Cordia*, 282-288; *C. lutea*, n = 36, count by Kyhos.]
- WOOD, C. E., JR. Lectotypification of generic names in floras. *Taxon* 16: 23-28. 1967.

Subfam. II. EHRETIOIDEAE Gürke in Engler &
Prantl, Nat. Pflanzenfam. VI. 3A: 86. 1897.

2. *Bourreria* P. Browne, Civ. Nat. Hist. Jamaica 168. 1756, nom. cons.⁷

Trees or shrubs. Leaves alternate, petiolate, entire, glabrous or scabrous to tomentose. Inflorescences few- to many-flowered, terminal, dichotomously branched, corymbose racemes, rarely solitary; flowers actinomorphic (regular), perfect. Calyx campanulate to tubular, glabrous [or pubescent] on the outside, usually densely pubescent on the inside, persistent, often rupturing in fruit; calyx teeth 2 to 5, valvate in bud. Corolla funnellform [campanulate or salverform], white [rarely yellow, red, or bluish], 5 lobed, the lobes imbricate in bud, spreading at anthesis. Stamens 5, epipetalous; filaments usually adnate to base of corolla tube; anthers oblong [or ovate], exserted to included. Ovary sessile, 4 loculate, the ovules solitary in each locule; style terminal, bifid [or undivided] at tip; stigmas 2 [rarely 1], truncate [capitate, or clavate]. Fruits drupaceous, ovoid to subglobose, consisting of 4 bony, often triquetrous, 1-seeded nutlets. Seeds attached laterally; endosperm fleshy; cotyledons flat. Base chromosome number 19. (Including *Crematoma* Miers, *Morelosia* La Llave & Lexarza.) TYPE SPECIES: *Cordia Bourreria* L. = *B. baccata* Raf.⁸ (Name commemorating Johann Ambrosius Beurer, 2 March 1716-27 June 1754, an apothecary of Nürnberg (Nuremberg) and a promoter of natural history.)

⁷In his original description of *Bourreria*, Browne stated that he named the genus after Mr. Bourer, whose name is correctly written as Beurer. Browne changed the spelling of the generic name to *Berueria* on page 492 of the index. A great deal of confusion in the orthography of *Bourreria* resulted from the earlier publication in 1755 of *Beueria* Ehret (= *Calycanthus* L.) and the later one in 1763 of *Beurreria* Jacq. The latter version is considered to be a "correction" of Browne's *Bourreria*. Several authors (e.g., Douglas, Laguna, Sprague, Rickett) have discussed at some length the orthography of the name, but none of them accepted the original version, *Bourreria*. Although the "erroneous" spelling of *Bourreria* was conserved after the Sixth International Botanical Conference at Amsterdam in 1935 (see Bull. Misc. Inf. Kew 1940: 121. 1940), there was no need to conserve the name in the first place. Whether or not the original version, *Bourreria*, is misspelled creates no problems, and the name should have been accepted as it appeared in the text rather than the index of the original publication. Rickett & Stafleu have correctly stated (p. 83) that *Bourreria* was conserved "probably by oversight," and Stearn indicated (p. 169) that "we are stuck with it."

⁸*Bourreria* has been listed with a conserved type, *B. succulenta*, in almost all editions of the International Code (ICBN, 1947 through 1983). However, the latest edition (1988) gives *B. baccata* Raf. as the type. This change in the typification of the genus was almost certainly taken from Stearn's work, in which it is stated for the first time that *B. baccata*, which is based on the Linnaean binomial *Cordia Bourreria* L., is the type of *Bourreria*.

About 50 species according to some authors (e.g., Correll & Correll, Willis), but more likely fewer, perhaps 30. The genus is distributed primarily in the West Indies and Mexico, with a few species endemic to portions of Central America and others with ranges that extend either north to southernmost Florida or south to northern South America. The transfer by Thulin of some tropical African species of *Ehretia* L. to *Bourreria* is discussed below. *Bourreria* is represented in the southeastern United States by three species that grow in Florida, as well as in portions of the West Indies.

Bourreria is a taxonomically difficult and poorly studied genus that is in need of a revisionary or monographic treatment. Many taxa are based on characters, the variation of which is either continuous or little understood. Field work might well resolve most problems that relate to the variation of characters and boundaries of species. The only comprehensive revision of *Bourreria* is Schulz's, which is unsatisfactory because he treated only the Caribbean taxa, adopted a somewhat narrow species concept, mishandled some of the nomenclatural problems, and misinterpreted the results of certain prior studies. He recognized three sections in his key but did not treat them in the text. It is beyond the scope of this flora to deal with the infrageneric classification of the genus as a whole. It is evident, however, that the three species occurring in Florida belong to sect. *BOURRERIA*.

The assignment of binomials to the three species of *Bourreria* that grow in Florida is difficult without the nomenclatural types. There is only a slight agreement among some of the 15 consulted floristic and revisionary works that have dealt with the Florida plants. Consequently, it is practical to minimize the number of taxa that are based on trivial differences.

Bourreria succulenta Jacq. (*B. revoluta* HBK., *B. succulenta* var. *revoluta* (HBK.) O. E. Schulz, *Ehretia havanensis* Roemer & Schultes, *B. havanensis* (Roemer & Schultes) Miers, *B. tomentosa* G. Don var. *havanensis* (Roemer & Schultes) Griseb., *B. ovata* Miers, *B.*

Browne's original description of the genus was based on a single species, *Bourreria arborea foliis ovatis alternis, racemis rarioribus terminalibus*. Linnaeus (Syst. Nat. ed. 10. 2: 936. 1759) based *Cordia Bourreria* on Browne's plant (Linnaean Herb. 254. 2), citing "fol. ovatis integerrimis, fl. subcorymbosis, calyce-laevis, Brown. Jam. 168. t. 15. fig. 2," but he also cited two other works that dealt with two unrelated species. The typification of *Bourreria* is therefore straightforward and poses no problems. Since the transfer of *Cordia Bourreria* would create a tautonym under *Bourreria*, the earliest available binomial that cites Linnaeus and/or Browne becomes the name of the type species. Stearn stated correctly that *B. baccata* is the earliest such name and should therefore be accepted as the correct name of the generic type. Rafinesque cited under *B. baccata* "E. bour. L.," which is *Ehretia Bourreria* (L.) L., a name based on *C. Bourreria*. The designation in all except the 1988 edition of the Code of *B. succulenta* as a conserved type was evidently wrong. Jacquin (Enum. Syst. Pl. Carib. 2, 14. 1760) did not cite either Browne or Linnaeus but gave, instead, under *B. succulenta* Commelin's plate 79, which represents a species quite different from *B. baccata*. Furthermore, Jacquin's (Select. Stirp. Amer. 44. 1763) citation under the amended *Bourreria succulenta* of Browne's polynomial and Linnaeus' *C. Bourreria* has no bearing on the typification of the genus because *B. succulenta* should be typified by Commelin's plant.

ovata Miers var. *hirtella* O. E. Schulz, *B. recurva* Miers, *Crematomia venosa* Miers, *B. venosa* (Miers) Stearn, *B. velutina* (DC.) Gürke var. *venosa* (Miers) O. E. Schulz), Bahama strongback, strongbark, is widespread throughout most of the West Indies and also occurs in portions of Mexico and Venezuela. It is common on limestone in hammock margins on many of the Florida Keys (Monroe County). According to Tomlinson, the species is somewhat weedy, apparently does not persist in dense, mature hammocks, and has been recorded from mainland Florida.

Bourreria succulenta is a shrub or a tree to 12 m high, with reddish-brown bark, broadly obovate or sometimes oblanceolate to orbicular, glabrous leaves (3-)4-8(-13) cm long and (1.5-)2.5-5(-7) cm wide, slender petioles (0.5-)1-1.8(-2.5) cm long, 20- to 80-flowered dichotomous cymes, a usually glabrous calyx, and yellow fruits that when fully mature become orange-red and 9-14 mm in diameter.

As interpreted here, *Bourreria succulenta* includes what various authors have called *B. ovata* and *B. revoluta*. All these plants have broad, glabrous leaves, long petioles, many-flowered inflorescences, and reddish drupes. Whether *B. revoluta* should be recognized as an infraspecific taxon of *B. succulenta*, as it was treated by Schulz, who was followed by others (e.g., Adams; Tomlinson; Long & Lakela), or reduced to synonymy can be settled by examination of the type specimens.

Plants of *Bourreria succulenta* that grow in the Bahamas, the Dominican Republic, and Jamaica have either a single stigma on an undivided style or a stigma on each of two styler branches. Stearn recognized plants with two stigmas as *B. venosa* and retained those with one in *B. succulenta*. Critical study of the two flower morphs shows that there are no other morphological characters associated with the differences in stigma number. Adams is fully justified in concluding (p. 626) that "the degree of division of the style is inconsistent even on the same plant, thus suggesting that these two species [*B. succulenta* and *B. venosa*] may not be really distinct." The Florida material that I have examined has flowers with two stigmas.

Bourreria cassinifolia (A. Rich.) Griseb. (*Ehretia cassinifolia* A. Rich., *Morelosia cassinifolia* (A. Rich.) Kuntze), smooth strongback, smooth strongbark, is a low, many-branched shrub with spatulate to oblanceolate or narrowly obovate leaves (0.6-)1-2(-2.5) cm long and (3-)6-9(-12) mm wide, conspicuously hispid upper leaf surfaces, short petioles 1-2(-3) mm long, one- or few-flowered inflorescences, and orange fruits 7-8 mm in diameter. It grows in pinelands on Big Pine Key, Monroe County, and in those of Long Pine Key in Everglades National Park, Dade County. *Bourreria cassinifolia* was first recorded for Florida by Small (1933). Ward & Fantz have indicated that it is now close to extinction in Florida because of habitat destruction. The species also occurs in Cuba.

The very short petioles, few-flowered cymes, and scabrous, small leaves that are characteristic of *Bourreria cassinifolia* are also found

in *B. divaricata* (DC.) G. Don, *B. Ekmanii* O. E. Schulz, *B. homalophylla* O. E. Schulz, *B. microphylla* Griseb., *B. pauciflora* O. E. Schulz, *B. setosohispida* O. E. Schulz, and *B. stenophylla* O. E. Schulz. The differences between these given by Schulz and by Alain are not convincing, and the whole may represent a complex of several infraspecific taxa that belong to one or two species. The earliest published binomial in this group is *B. divaricata*. Because of the paucity of material at my disposal, it is not possible at present to define the boundaries of taxa in this complex.

The third species in Florida, *Bourreria radula* (Poiret ex Lam.) G. Don (*Ehretia radula* Poiret ex Lam., *B. havanensis* (Roemer & Schultes) Miers var. *radula* (Poiret ex Lam.) A. Gray, *Cordia floridana* Nutt.), rough strongback, rough strongbark, is known only from old collections that were all made in dry hammocks on Key West, Monroe County. Tomlinson, who listed the plant as *B. succulenta* var. *revoluta*, suggested that it is very rare or perhaps has disappeared in the wild. The species is also reported to grow in Hispaniola, but its status there is not known.

Bourreria radula is a small tree that in leaf morphology and number of flowers per inflorescence is intermediate between *B. cassinifolia* and *B. succulenta*. It has strigose, oblong-obovate to obovate leaves (1.4–)2.5–4.5(–6) cm long, and (0.7–)1.2–3(–3.5) cm wide, conspicuous pedicels (2–)3–7 mm long, 5–30-flowered cymes, and orange fruits 9–14 mm in diameter. Several authors (e.g., Small, 1933; Lakela & Craighead) have recognized this species as *B. revoluta*, while others (e.g., Schulz; Long & Lakela; Tomlinson) have treated it as a variety of *B. succulenta*. As indicated by Ward & Fantz, however, *B. revoluta* was described as having glabrous leaves, whereas *B. radula* has an upper leaf surface that is strigose (trichomes bulbous-based).

Bourreria is a well-defined genus that is easily distinguished from the closely related *Ehretia* in having closed buds, valvate, 2–5-lobed calyces, large corollas 8–48 mm long, entire leaves, and hard endocarps that separate at maturity into four 1-seeded units. In contrast, *Ehretia* has open buds, open or imbricate, 5-lobed calyces, small corollas (to 6 mm long), usually dentate or serrate leaves, and endocarps that usually split at maturity into two 2-seeded units. Thulin has recently evaluated the boundaries between the two genera and transferred to *Bourreria* four African species previously placed in *Ehretia*, as well as described a new species in the former. On the basis of the generic differences above, these African species are perhaps appropriately retained in *Ehretia*. They are disjunct from *Bourreria*, which is otherwise Caribbean and Central American, and their nearest relatives have not yet been determined. The African species form a monophyletic group and differ from *Bourreria* in having urceolate or campanulate instead of rotate corollas.

The reproductive biology of *Bourreria* is poorly studied and neither heterostyly nor dioecy has been reported (Percival). The red-flowered *B. rubra* E. J. Lott & J. S. Miller, a Mexican species endemic to coastal

Jalisco, probably is pollinated by hummingbirds (Trochilidae). Most species of the genus, however, have white flowers, although there are a few that are yellow, and Alain indicated that *B. rotata* (DC.) I. M. Johnston has blue flowers. Flower size varies greatly among the different species. The largest flowers are found in the Costa Rican *B. Quirosii* Standley (ca. 3.5 cm long) and the Central American *B. costaricensis* (Standley) A. Gentry (2.5–5 cm long); *B. oxyphylla* Standley has the smallest (8–12 mm long) (J. S. Miller). Unfortunately, the pollination ecology of none of the species has been studied.

The genus has not been surveyed adequately for chromosome numbers, and only *Bourreria Quirosii*, which was reported to have $n = 19$ (Bawa), has been studied. Nowicke & Miller (1989) have shown that the pollen of *B. oxyphylla* is tricolporate and the colpi are bordered by meridional ridges that are separated by intercolpar concavities. The foot layer is thickest at the center of each ridge and becomes very thin or is nearly absent in the intercolpar concavities. *Bourreria* resembles *Ehretia* palynologically, but both genera are as yet poorly studied.

Record & Hess observed no anatomical peculiarities in the wood anatomy of *Bourreria*, but Barajas Morales (1983) found that wood of the Mexican *B. Purpusii* Brandege contains prismatic calcium oxalate crystals and the vessels have vestured pits.

Although a few species of *Bourreria* are used locally for various purposes, the genus is not economically important. Hedrick indicated that the fruits of *B. succulenta* are sweet and edible. Altschul, Ayensu, and Morton all stated that the plant (as *B. ovata*) is used in the Bahamas to prepare a tea, believed by some to strengthen the back, hence the common name strongback. Ayensu listed several other medicinal attributes of the species. The highly scented flowers of the Mexican *B. Huanita* (La Llave & Lexarza) Hemsley are an ingredient of a fermented beverage and are also used for perfuming tobacco and flavoring sweetmeats and conserves (Record & Hess). Historians consider *B. Huanita* as the cause of a war in 1496 between two villages, the "king" of one of which wanted the plant for his celebrated garden (Douglass; Record & Hess).

REFERENCES:

Under family references see ALTSCHUL; AYENSU; BAILLON; BARAJAS MORALES (1981, 1983); BENTHAM & HOOKER; DE CANDOLLE; CHAPMAN; CORRELL & CORRELL; T. S. ELIAS; GRAF; HARRAR & HARRAR; HARTWELL; HEDRICK; HOWARD; JOHNSTON (1949); LAKELA & CRAIGHEAD; LITTLE (1978, 1979); LONG & LAKELA; J. S. MILLER (1988, 1989b); R. B. MILLER; MORTON; NOWICKE; NOWICKE & MILLER (1979); PITOT; POLLARD & AMUTI; RECORD & HESS; SARGENT; STANDLEY; SMALL (1903, 1913, 1933); WARD & FANTZ; and WILLIS.

ADAMS, C. D. Flowering plants of Jamaica. 848 pp. Mona, Jamaica. 1972. [*Bourreria*, 625, 626.]

ALAIN, Hno. Boraginaceae. Fl. Cuba. 4: 252–278. 1957. [*Bourreria*, 267–272; 18 species recognized.]

- . Novelties in the Cuban flora. XIV. *Phytologia* 8: 369, 370. 1962. [*B. turquinensis*, sp. nov.]
- BAWA, K. S. Chromosome numbers of tree species of a lowland tropical community. *Jour. Arnold Arb.* 54: 422–434. 1973. [*B. Quirosii*, 430, $n = 19$.]
- BRITTON, N. L. North American trees. x + 894 pp. New York. 1908. [*Bourreria*, 821, 822; *B. havanensis* and *B. virgata* in Florida; *B. succulenta* as the generic type.]
- DOUGLAS, M. The huanita. *Jour. N. Y. Bot. Gard.* 47: 112–118. 1946. [*B. Huanita*; history, botany, economic importance, role in a local war.]
- GENTRY, A. H. *Schlegelia costaricensis*: a familial transfer to Boraginaceae. *Phytologia* 26: 67, 68. 1973. [= *B. costaricensis*, comb. nov.]
- LAGUNA, A. R. Estado actual de nuestros conocimientos acerca de la planta conocida con el nombre de "huanita." *Anal. Inst. Biol. México* 2: 197–206. 1931. [*B. Huanita*; historical account, morphology, cultivation, economic botany, distribution.]
- LOTT, E. J., & J. E. MILLER. *Bourreria rubra* (Boraginaceae), a new species from coastal Jalisco, Mexico. *Ann. Missouri Bot. Gard.* 73: 216–218. 1986. [Species unique in the genus for its red flowers; illustration.]
- MIERS, J. On the Ehretiaceae. *Ann. Mag. Nat. Hist.* IV. 3: 106–112, 199–201, 300–313. 1869. [Fifteen species of *Bourreria*, 199, 200, and 19 of *Crematomia*, 300–313; *Ehretia*.]
- PERCIVAL, M. Floral ecology of coastal scrub in Southeast Jamaica. *Biotropica* 6: 104–129. 1974.
- RAFINESQUE, C. S. *Sylva Telluriana mantis[s]a synopt[ica]*. 184 pp. Philadelphia. 1838. [*Bourreria*, 42.]
- RICKETT, H. W. On orthographic change. *Taxon* 3: 138–140. 1954. [*Bourreria*, 138.]
- & F. A. STAFLEU. Nomina generica conservanda et rejicienda spermatophytorum IV. *Taxon* 9: 67–86. 1960. [*Bourreria*, 83.]
- SARGENT, C. S. The silva of North America. Vol. 6. vii + 124 pp. pls. 252–300. Boston and New York. 1894. [*Bourreria*, 75–78, pls. 285, 286; *B. ovata* (as *B. havanensis*).]
- SCHULZ, O. E. *Bourreria* (as *Beureria*) in I. URBAN, *Symb. Antill.* 7: 45–71. 1911. [Eighteen species recognized.]
- SPRAGUE, T. A. The correct spelling of certain generic names — III. *Bull. Misc. Inf. Kew* 1928: 337–365. 1928. [*Bourreria* (as *Beureria*), 347, 348.]
- STANDLEY, P. The huanita tree of Mexico. *Trop. Woods* 28: 14, 15. 1931. [*B. Huanita*; discovery, nomenclature.]
- STEARNS, W. T. Taxonomic and nomenclatural notes on Jamaican gamopetalous plants. *Jour. Arnold Arb.* 52: 614–648. 1971. [*Bourreria*, 619–626; history of the genus, treatment of four species, keys, notes, maps.]
- THULIN, M. *Bourreria* (Boraginaceae) in tropical Africa. *Nordic Jour. Bot.* 7: 413–417. 1987. [Five species recognized; generic boundaries between *Bourreria* and *Ehretia*.]
- TOMLINSON, P. B. The biology of trees native to tropical Florida. [ix] + 480 pp. Allston, Massachusetts. 1980. [*Bourreria*, 108–112; *B. ovata*, *B. succulenta* var. *revoluta*, and *B. cassinifolia* recognized, the first two illustrated.]

Subfam. III. HELIOTROPIOIDEAE Gürke in Engler & Prantl, Nat. Pflanzenfam. VI. 3A: 90. 1897.

3. *Tournefortia* Linnaeus, Sp. Pl. 1: 140. 1753; Gen. Pl. ed. 5. 68. 1754.

Woody vines [shrubs, or rarely small trees], variously pubescent [or glabrous]. Leaves alternate [rarely opposite], distinctly petiolate, broad, entire. Inflorescences terminal or axillary, consisting of scorpioid cymes or racemes grouped in usually dichotomous, few- to many-branched panicles; flowers perfect, actinomorphic (regular). Calyx persistent, usually 5 lobed, one lobe often longer than the others. Corolla white [green, or yellowish], small, tubular, usually 5 lobed, the tube short or long, pubescent [or glabrous], the lobes spreading, frequently conduplicate, glabrous on the inside. Stamens 5, usually included, inserted on the corolla tube, the filament very short or almost lacking. Ovary ovoid to globose, 4 locular, sometimes slightly 4 lobed; style solitary, terminal [rarely obsolete]; stigma conical [or peltate], fertile on the sides, often bifid at the sterile apex. Fruits drupes, usually white, entire, or somewhat lobed at maturity, glabrous or pubescent, with juicy mesocarp, later drying and breaking up into 2 or 4 bony endocarps each containing 1 or 2 seeds or sometimes with empty cavities. Endosperm thin; cotyledons flat. (Including *Myriopus* Small, *Oskampia* Raf., *Pittonia* Miller, *Tetrandra* (DC.) Miquel, *Verrucaria* Medicus non Wegg.) LECTOTYPE SPECIES: *T. hirsutissima* L.;⁹ see Britton & Millspaugh, Bahama Fl. 361. 1920, and Johnston, 1930. (Name commemorating the French botanist Joseph Pitton de Tournefort, 5 June 1656–28 Dec. 1708.)

A taxonomically difficult and poorly studied genus of about 150 species distributed primarily in the Neotropics, with the center of greatest diversity in South America. Only about 12 species occur in the Old World (Johnston, 1935). *Tournefortia* is represented in the southeastern United States by two indigenous species that are also widely distributed in tropical America.

The sectional classification of *Tournefortia* is problematic, and three of the five sections recognized by De Candolle are now believed to belong to other genera. The monotypic sects. *Mallota* A. DC. and *Arguzia* (Amman) DC. are reduced to the synonymy of *Argusia*, whereas sect. *Messerschmidia* (*sensu* DC.) is more appropriately placed in *Heliotropium* (Johnston, 1930). The two remaining sections, sects. *Pittoniae* HBK. and *Tetrandra* DC., were combined by Johnston (1935) as sect. *Eutournefortia* (= sect. *Tournefortia*).

⁹Hitchcock & Green overlooked the earlier typification of Britton & Millspaugh, selecting instead *Tournefortia volubilis* as the generic type. They justified their selection on the grounds (p. 128) that it "was the species best known to Linné." As clearly demonstrated by Johnston (1930), however, the fruit characteristics of *T. volubilis* do not agree with the original generic description, and the genus was based primarily on *T. hirsutissima*.

Johnston (1930) divided the genus into two well-defined sections. Members of sect. *TOURNEFORTIA* have free anthers, straight embryos, and obscurely lobed or unlobed fruits that break up at maturity into one- or two-seeded irregular nutlets. In contrast, in sect. *CYPHOCYEMA* Johnston the anthers are apically connate, the embryos curved, and the fruits conspicuously lobed and separating at maturity into four similar one-seeded nutlets. The latter section is centered in South America, and apparently only *T. volubilis*, the sectional type, and *T. maculata* Jacq. are widespread elsewhere in tropical America.

Tournefortia hirsutissima L. (*Messerschmidia hirsutissima* (L.) Roemer & Schultes, *T. elliptica* Maretna & Gal., *T. Schomburgkii* DC.) is distributed in southern Florida, the West Indies, Mexico, Central America, and northern South America. It is occasional in Florida, where it grows in subtropical hammocks in portions of Collier, Dade, and Monroe counties. It has also been reported from Hendry County (Wunderlin). The plant occurs in diverse habitats from sea level in Florida to altitudes as high as 2000 m elsewhere (J. S. Miller).

Tournefortia hirsutissima is a sprawling shrub or woody vine with lanceolate-ovate to elliptic, strigose to hispid leaves 7–15(–20) cm long, sessile flowers with white, ovate-lobed corollas, and white, ovoid to spherical, strigillose drupes. The species is most closely related to the widespread *T. bicolor* Sw., which was reduced to a form of *T. hirsutissima* by Nash & Moreno, but evidence given by J. S. Miller supports its maintenance as a distinct species.

Tournefortia volubilis L. (*Myriopus volubilis* (L.) Small, *T. poliochros* Sprengl, *M. poliochros* (Sprengel) Small; see Johnston (1949) and Gibson for ten additional synonyms), soldier bush, grows in coastal hammocks and on shell mounds in Brevard, Dade, and Monroe counties, Florida. It is apparently more abundant in the Everglades National Park and on some of the Keys than elsewhere in these counties. The plant is widespread in the West Indies, Mexico, Central America, and northern and northwestern South America.

Tournefortia volubilis is extremely variable in leaf shape, size, and pubescence, but none of the variants merits recognition. Small (1933), as well as several other workers (e.g., Alain, Correll & Correll, Lakela & Craighead, Long & Lakela) who have followed his account, recognized a leaf variant of this species as *T. poliochros*, which was said to differ in having narrowly lanceolate leaves with an acuminate apex and a densely pubescent, somewhat canescent lower surface. *Tournefortia volubilis* was said to have ovate to elliptic or rarely lanceolate leaves with obtuse apex and glabrous to sparsely pubescent lower surface, but these differences can be found in various combinations throughout the range of *T. volubilis*. In concurrence with Ward & Fantz and Wunderlin, *T. poliochros* is treated here as a synonym of *T. volubilis*.

Tournefortia volubilis is distinctive among the other Boraginaceae of the Southeastern States in being a woody vine with petiolate leaves and in having dichotomously branched panicles of scorpioid cymes,



FIGURE 2. *Argusia* and *Tournefortia*. a-i, *A. gnaphalodes*: a, flowering and fruiting branchlet, $\times 1/2$; b, flower, $\times 4$; c, anther, $\times 15$; d, gynoecium with disc, $\times 12$; e, nearly mature fruit, $\times 2$; f, endocarp of mature fruit, $\times 6$; g, diagrammatic vertical section of fruit showing bony endocarp (coarse hatching), corky tissue (fine hatching), fleshy portions (unshaded), two seeds with endosperm (stippled) and embryos, $\times 3$; h, diagrammatic cross section of fruit showing four locules (two with aborted seeds), the details as in "g" and the section cut at level shown by arrow in g, $\times 4$; i, half of endocarp (seen from the axis of fruit) after removal of fragile parts of endocarp and soft tissues of fruit, $\times 4$. j-p, *T. volubilis*: j, branchlet with inflorescences—note sympodial growth, $\times 1/2$; k, flower, $\times 12$; l, anther, $\times 20$; m, gynoecium, $\times 15$; n, immature fruit with only two ovules fertilized, $\times 6$; o, mature fruit with four ovules fertilized, $\times 6$; p, one of four endocarps from fruit (should be rotated 90° clockwise), $\times 12$. q, *T. hirsutissima*: one of four endocarps from fruit, $\times 6$.

tubular corollas with linear-lanceolate to subulate lobes, apically connate anthers, and fleshy, conspicuously four-lobed, white drupes with dark brown to black spots at the apex.

Tournefortia is a well-marked genus that differs from other members of the subfamily Heliotropioideae in having fleshy, drupaceous fruits and in habit being primarily woody vines, although some species are shrubs or small trees. The presumably related *Argusia* (q.v.) has corky fruits and differs in indumentum, whereas *Heliotropium* is primarily herbaceous and has dry fruits.

Tournefortia, probably the third largest genus in the Boraginaceae, is one of the least studied for chromosome numbers, chemistry, floral biology, embryology, dispersal ecology, and anatomy, and the scant data do not permit any meaningful generalizations. Apparently the chromosomes of only *T. paniculata* Cham., $n = 12$, have been counted (Di Fulvio), and the alkaloids of *T. sarmentosa* Lam. studied. The latter contains the pyrrolizidine alkaloid supinine (Smith & Culvenor).

Nowicke & Skvarla recognized four pollen types among the 62 species of *Tournefortia* and the three of *Argusia* (as *Messerschmidia*) that they surveyed. Pollen of the first type, which was found in 46 species (including those of *Argusia*), is subprolate and has 3-colporate apertures alternating with three pseudocolpi and a psilate ectexine. The second type, found in 12 species, is subprolate, 3-colporate, psilate at the expanded poles, and verrucate at the equator, while grains of the third type, in five species, are spheroidal and have 3-porate apertures and a clavate ectexine. The remaining type, seen in only two species, is suboblate and has 3- or 4-colporate apertures and a finely rugose to psilate ectexine. Nowicke & Skvarla noted that pollen of the three species of *Argusia* is similar to that of the first group and suggested that the palynological evidence neither supports nor negates the placement of these in a separate genus. They also considered pollen of the first type to be basic for *Tournefortia* because it is randomly distributed in the genus and is found in the largest and most diversified group of species. The occurrence in *Heliotropium* of a dominant pollen type similar to that of *Tournefortia* was taken as strong support for the close association of the two genera. Pollen data, however, do not support Johnston's (1930) division of *Tournefortia* into two sections, since members of both sections have similar pollen types.

Record & Hess studied the wood anatomy of *Tournefortia glabra* L., *T. hirsutissima*, *T. racemosissima* Krause, and *T. rugosa* Willd., described the wood texture and finish, and gave measurements for various tissue components of the xylem. No anatomical peculiarities were found. Metcalfe & Chalk reported the occurrence of storied rays in *Tournefortia*, but Gottwald found no trace of these in more than 30 samples studied. No vested pits were found in the genus (R. B. Miller).

Various medicinal values have been attributed to the species of *Tournefortia* as used locally (Ayensu, Perry), but it is doubtful that the genus is of any economic importance. Several authors have stated that the powdered leaves are used to treat sores and boils.

REFERENCES:

- Under family references see ADAMS; ALAIN; AYENSU; BAILLON; BENTHAM & HOOKER; BULL *et al.*; I. H. BURKILL; DE CANDOLLE; CHAPMAN, CORRELL & CORRELL; CORRELL & JOHNSTON; GOTTFELD; GRAHAM & JARZEN; HARTWELL; HOWARD; JOHNSTON (1936); JOHNSTON *et al.*; LAKELA & CRAIGHEAD; LONG & LAKELA; LUBBOCK; METCALFE & CHALK; J. S. MILLER; R. B. MILLER; MITCHELL & ROOK; NASH & MORENO; NOWICKE; PERRY; POLLARD & AMUTI; QUISUMBING; RECORD & HESS; SMALL (1903, 1913, 1933); L. B. SMITH; SMITH & CULVENOR; STANDLEY; STEARN; WARD & FANTZ; WIGGINS; and WUNDERLIN.
- BRADE, A. C. Os generos *Cordia* e *Tournefortia*. Bol. Mus. Nac. Rio de Janeiro 8: 13-47. 2 pls. 1932. [Seventeen species of *Tournefortia* in Brazil; keys to sections and species, synonymy, illustrations.]
- BRITTON, N. L., & C. F. MILLSPAUGH. The Bahama flora. viii + 695 pp. New York. 1920. [*Tournefortia*, 361, 362, including typification of the genus.]
- DI FULVIO, T. E. Recuentos cromosómicos en angiospermas argentinas. Kurtziana 4: 87-90. 1967. [*T. paniculata* var. *austrina*, *n* = 12.]
- GENTRY, A. H. New species of *Gibsoniothamnus* (Scrophulariaceae/Bignoniaceae) and *Tournefortia* (Boraginaceae) from eastern Panama and the Chocó. Ann. Missouri Bot. Gard. 64: 133-135. 1977. [*T. tacarcunensis*, sp. nov.]
- GIBSON, D. N. Two new Guatemalan *Tournefortias*. Fieldiana Bot. 32: 65-68. 1969. [*T. elongata* and *T. longiloba*, spp. nov.; illustrations.]
- HITCHCOCK, A. S., & M. L. GREEN. Standard-species of Linnean genera of Phanerogamae (1753-54). Pp. 111-199 in Internatl. Bot. Congress, Cambridge, England, 1930. Nomenclature. Proposals by British botanists. London. 1929. [*Tournefortia*, 128.]
- JOHNSTON, I. M. Studies in the Boraginaceae, —VIII. I. Observations on the species of *Cordia* and *Tournefortia* known from Brazil, Paraguay, Uruguay and Argentina. Contr. Gray Herb. 92: 1-89. 1930. [*Tournefortia*, 66-89; typification of the genus, 17 species in two sections, keys, nomenclature, notes, distributions.]
- . Studies in the Boraginaceae, XI. 1. The species of *Tournefortia* and *Messerschmidia* in the Old World. Jour. Arnold Arb. 16: 145-168. 1935. [Twelve species of *Tournefortia*; key, notes, nomenclature.]
- . Studies in the Boraginaceae, XVIII. Boraginaceae of the southern West Indies. *Ibid.* 30: 111-138. 1949. [*Tournefortia*, 129-133; eight species (incl. *T. hirsutissima* and *T. volubilis*); keys, notes, nomenclature.]
- MCMULLEN, C. K. Breeding systems of selected Galápagos Islands angiosperms. Am. Jour. Bot. 74: 1694-1705. 1987. [*T. psilostachya*, *T. pubescens*, and *T. rufosericea* are self-compatible, 1699.]
- MILLER, J. S. Two new species of *Tournefortia* (Boraginaceae) from Colombia. Ann. Missouri Bot. Gard. 76: 619-622. 1989. [*T. Brantii* and *T. spicata*, spp. nov.]
- NOWICKE, J. W. Three new species of *Tournefortia* (Boraginaceae) from the Andes and comments on the manuscripts of E. P. Killip. Bull. Torrey Bot. Club 101: 229-234. 1974. [*T. Killipii*, *T. latisejala*, *T. pauciflora*, spp. nov.; illustrations, scanning-electron micrographs of pollen and leaf trichomes.]
- & J. J. SKVARLA. A palynological investigation of the genus *Tournefortia* (Boraginaceae). Am. Jour. Bot. 61: 1021-1036. 1974. [Pollen morphology of 65 species, including three of *Argusia*; four pollen types recognized, data support a close relationship to *Heliotropium*.]
- PROCTOR, G. R. More additions to the flora of Jamaica. Jour. Arnold Arb. 63: 199-315. 1982. [*Tournefortia*, 295-297; *T. smaragdina*, sp. nov.]

QUIROZ-GARCÍA, D. L., & R. PALACIOS-CHÁVEZ. Catálogo palinológico para la flora de Veracruz. No. 32. Familia Boraginaceae. Género *Tournefortia*. (English summary.) *Biotica* 10: 55-61. 1986. [Seven species, including *Argusia gnaphalodes*, *T. hirsutissima*, and *T. volubilis*; see NOWICKE & SKVARLA; 8 pls.]

4. *Argusia* Boehmer in Ludwig, Defin. Gen. Pl. ed. Boehmer. 507. 1760.

Shrubs [herbs or trees], densely white-sericeous [strigose or hispid-villous]. Leaves fleshy [or not], sessile [or nearly so], narrowly linear [lanceolate, oblong, obovate, or oblanceolate], cuneate to attenuate at base. Inflorescences ebracteate, dichotomously branched, 1-sided, densely flowered cymes, glomerulate [corymbose or paniculate], not elongated [or greatly expanded] in fruit; flowers sessile, white, fragrant. Calyx 5 parted almost to base, densely appressed-sericeous [or strigose] on the outside, glabrous within. Corolla tubular [or funneliform], appressed tomentose [or strigose] on the outside of tube, glabrous within and without faucal scales, the lobes lanceolate [ovate, oblong, or sub-orbicular], conduplicate in bud. Anthers oblong, mucronate, included, attached below the corolla throat by a very short filament. Style undivided, terminal, short, included; stigma frustum shaped, receptive in a ring about the base, the sterile portion thick and slightly 2 lobed. Fruit glabrous, drupaceous, dry when mature, the mesocarp corky, vesicular, the endocarp woody, divided into 2 portions each with 2 one-seeded locules that are usually separated by a deep groove. Base chromosome numbers 13, 14. (Including *Mallotonia* (Griseb.) Britton, *Tournefortia* L. sect. *Mallotonia* Griseb., *Tournefortia* sect. *Argusia* (Amman) DC., *Messerschmidia* Hebenstreit.) TYPE SPECIES: *Tournefortia sibirica* L. = *A. sibirica* (L.) Dandy. (Named after the Argun River, a headstream of the Amur River on the border between Manchuria and the U.S.S.R.) — SEA LAVENDER.

A small genus of three species, of which one is indigenous to tropical America, another is widespread in the Old World tropics, and a third is a Eurasian plant. All three species are strand plants, but *Argusia sibirica* is also an inland species that grows on saline sand between 40° and 56° N from southern Russia and the shores of the Black Sea eastward into central Asia and to coastal northern China and Japan. It is a waif in North America and has been either introduced repeatedly or has persisted on ballast at Portland, Oregon (Cronquist). The species differs from other members of *Argusia* in being a rhizomatous herb, instead of a shrub or tree.

Argusia argentea (L. f.) Heine is a strand shrub or tree to ten meters tall and is widely distributed on islands of the Pacific and Indian oceans. It is less common on the continental coasts of northern Australia, eastern Africa, and southern and eastern Asia.

Argusia gnaphalodes (L.) Heine (*Heliotropium gnaphalodes* L., *Tournefortia gnaphalodes* (L.) R. Br. ex Roemer & Schultes, *Mallotonia gnaphalodes* (L.) Britton, *Messerschmidia gnaphalodes* (L.)

Johnston), sea lavender, lavender, $2n = 28$, is a widespread strand plant in the West Indies, with outlying populations in northern Venezuela, the Caribbean coast of Central America, southern Florida, and Bermuda. In Florida the species is common (at least formerly) along the coasts of the Florida Keys (Monroe County) and is rare northward along the west coast to Collier County (Lakela & Craighead) and along the east coast to Cape Canaveral, Brevard County (Craig; Ward & Fantz; Wunderlin). *Argusia gnaphalodes* is a shrub to three meters tall, having densely sericeous foliage with silky gray pubescence, sessile, linear to linear-spatulate, succulent leaves, densely flowered glomerulate cymes that hardly elongate in fruiting, and glabrous, dark brown fruits with a corky exocarp. Since it grows primarily on the outer edge of salt flats and on the front line of coastal dunes (Ward & Franz), it receives continual sea spray.

It is controversial whether *Argusia* should be recognized as a distinct genus or reduced to the synonymy of *Tournefortia*. De Candolle's treatment of the three species in three sections of *Tournefortia*, two of which were monotypic, was followed by Gürke but was not accepted by most students of the family. Perhaps most of the confusion regarding the generic status of this group has resulted from Johnston's (1930, 1935, 1949, 1951a) four inconsistent treatments, in which he placed the three species initially in *Tournefortia*, then in *Messerschmidia*, then back in *Tournefortia*, and still later in *Messerschmidia*.

Messerschmidia should be rejected because it is based on the same type as the earlier and validly published, legitimate *Argusia*. All three species of *Argusia* differ markedly from *Tournefortia*, in which they were previously placed, in that they grow in strand habitats or in saline sand, have a silky covering of slender trichomes, and have dry fruits with a corky exocarp. In contrast, species of *Tournefortia* have fleshy drupes and different types of trichomes and occupy other habitats. Johnston (1935, p. 62) emphasized that the pronounced development of corky exocarp in species of *Argusia* (as *Messerschmidia*) "sets them off not only from all species of *Tournefortia* but from all other Boraginaceae as well." He also pointed out (1951a) that the genus is closer to *Heliotropium* than to *Tournefortia*.

Nowicke & Skvarla, who studied the palynology of 65 species of *Tournefortia*, found that pollen grains of the three species that are recognized here as *Argusia* are subprolate and 3-colporate and have three well-developed, alternating pseudocolpi. In this they resemble 43 species of *Tournefortia*. On the basis of these findings, Nowicke & Skvarla argued that palynology neither supports nor denies the recognition of *Argusia* (as *Messerschmidia*) as a genus distinct from *Tournefortia*. However, the tremendous diversity in the pollen of *Tournefortia* raises more questions about the limits of this genus than casting doubts on the distinctness of *Argusia*. Ahn & Lee confirmed Nowicke & Skvarla's findings about the pollen of *A. sibirica*, and Leopold (in Muller) reported pollen of *A. argentea* from the Miocene of the Marshall Islands, South Pacific.

Johnston's position (1935, 1951a) regarding the uniqueness of fruit morphology of *Argusia* is probably justified, and the heterogeneity in habit and pubescence do not support Nowicke & Skvarla's argument for retaining the species in *Tournefortia*. However, Verdcourt expressed concern about the floral heterogeneity of *Argusia*, particularly the insertion of staminal filaments on the corolla tube and the differences among species in the shape of the stigma.

The problem of generic boundaries between *Argusia* and *Tournefortia* was further complicated by Pôpov's (1953) transfer of the Central Asian *Heliotropium sogdianum* Bunge to *Tournefortia* and Riedl's (1967) transfer of it to *Messerschmidia*. As suggested by Verdcourt, the species is anomalous in both *Argusia* and *Heliotropium*, and as interpreted here, in *Tournefortia*. In the final analysis, the merging of *Argusia* with *Tournefortia* would disrupt the morphological, but not the palynological, homogeneity of the latter, whereas its maintenance as a distinct genus, as I and many recent students of the Boraginaceae would prefer, raises a number of questions regarding the phylogeny of *Argusia*, the evolution of its fruit type, and the diversity in its habit and flower morphology. Perhaps the comparative fruit anatomy of *Argusia* might help in establishing whether such corky fruits are truly unique in the Boraginaceae, as suggested by Johnston (1935a), or whether they have evolved independently.

Chromosome numbers have been reported for *Argusia gnaphalodes*, $2n = 28$, as *Mallotonia* (Hill) and for *A. sibirica*, $2n = 26$, as *Tournefortia Argusia* (L.) Roemer & Schultes and *T. sibirica* (Bolkhovskikh *et al.*). No counts have been made for *A. argentea*. The slight aneuploid difference in the counts above might support the placement of the two species in one genus, but more counts are needed before any meaningful conclusions can be reached.

The floral biology, embryology, and chemistry of *Argusia* have not been studied, and only in *A. sibirica* has one pyrrolizidine alkaloid, turneforcline, been determined (Bull *et al.*). Leaf anatomy of *A. gnaphalodes* was studied by Harshberger, who observed upper and lower palisade layers, each two cells thick.

Argusia argentea and *A. gnaphalodes* are respectively abundant along the tropical beaches of the Old and New Worlds. They grow slightly above the high tide line, where they are often subjected to salt spray. Their salt tolerance and fruit dispersal by ocean currents is further demonstrated by the ability of their corky fruits to float in sea water for many days, by the inhibition of germination by sea water, and by the retention of seed viability for more than 120 days (Lesko & Walker). Seed germination usually takes place shortly after rain falls on fruits previously exposed to sea water. It is not known whether the germination ecology of *A. sibirica* resembles that of the other two species of the genus.

Argusia argentea and *A. gnaphalodes* are useful plants for the control of erosion along beaches and coastal dunes, and the latter has occasionally been cultivated in Florida as an ornamental (Craig). The dried

leaves of *A. argentea* are smoked in the Seychelles and some other portions of tropical Asia (Lewis & Elvin-Lewis; Zeven & De Wet). Several medicinal properties for these two species were listed by I. H. Burkill and Ayensu. The wood of *A. argentea* is used for making diving goggles (Reis & Lipp) and in Guam for shoe-lasts (I. H. Burkill).

REFERENCES:

- Under family references see ADAMS; ALAIN; AYENSU; BOLKHOVSKIKH *et al.*; BULL *et al.*; I. H. BURKILL; DE CANDOLLE; CORRELL & CORRELL; GIBSON; GÜRKE; HEGNAUER (1964); HOWARD; JOHNSTON (1949, 1951a); LEWIS & ELVIN-LEWIS; J. S. MILLER; NASH & MORENO; POPOV (1953); PROCTOR; REIS & LIPP; RIEDL (1967); SMALL (1903, 1933); STANDLEY; VERDCOURT; WARD & FANTZ; WUNDERLIN; and ZEVEN & DE WET.
- CRAIG, R. M. Threatened sea-lavender. Pp. 101, 102 in D. B. WARD, ed., *Rare and endangered biota of Florida*. Vol. 5. Plants. Gainesville, Florida. [1978.] [*A. gnaphalodes* (as *Mallotonia*); description, range, habitat, status, recommendations.]
- CRONQUIST, A. Boraginaceae. In: C. L. HITCHCOCK, A. CRONQUIST, M. OWNBEY, & J. W. THOMPSON, *Vascular Pl. Pacific Northwest* 4: 175-244. 1959. [*A. sibirica* (as *Tournefortia*), 214.]
- DANDY, J. Note on *Argusia* Boehmer (Boraginaceae). *Bot. Jour. Linn. Soc.* 65: 256. 1972. [Generic name *Messerschmidia* reduced to synonymy of *Argusia*.]
- EDMONDSON, J. R. *Tournefortia*. In: P. H. DAVIS, ed., *Fl. Turkey* 6: 246, 248. 1978. [*A. (as Tournefortia) sibirica*.]
- GUPPY, H. B. Plants, seeds, and currents in the West Indies and Azores. *Frontisp.* + xi + 531 pp. 3 maps. London. 1917. [*A. argentea* and *A. gnaphalodes* (as *Tournefortia*), 247-251; buoyancy, survival, dispersal.]
- HARSHBERGER, J. W. The comparative leaf structure of the sand dune plants of Bermuda. *Proc. Am. Philos. Soc.* 47: 97-110. pls. 1-3. 1908. [*A. gnaphalodes* (as *Tournefortia*), 108, 109, fig. 17.]
- HEINE, H. Boraginaceae. In: A. AUBRÉVILLE & J.-F. LEROY, eds., *Fl. Nouv. Calédonie & Depend.* 7: 95-118. 1976. [*Argusia*, 108-112; new combinations, generic limits, treatment of *A. argentea*.]
- HILL, M. In: Chromosome number reports LXXXIV. *Taxon* 33: 536-539. 1984. [*A. gnaphalodes* (as *Mallotonia*), 537, n = 14.]
- JOHNSTON, I. M. Studies in the Boraginaceae.—VIII. *Contr. Gray Herb.* 92: 1-95. 1930. [*Argusia* (as *Messerschmidia*) united with *Tournefortia*, 72-74.]
- . Studies in the Boraginaceae, XI. 1. Species of *Tournefortia* and *Messerschmidia* in the Old World. *Jour. Arnold Arb.* 16: 145-165. 1935. [*Messerschmidia*; generic status, three species recognized, synonymy, key; 161-165; *A. gnaphalodes* (as *Messerschmidia*).]
- LESKO, G. L., & R. B. WALKER. Effect of sea water on seed germination in two Pacific atoll beach species. *Ecology* 50: 730-734. 1969. [*A. argentea*, dispersal, mobility, germination.]
- NOWICKE, J. W., & J. J. SKVARLA. A palynological investigation of the genus *Tournefortia* (Boraginaceae). *Am. Jour. Bot.* 61: 1021-1036. 1974. [*A. argentea*, *A. gnaphalodes*, and *A. sibirica* (as *Tournefortia*).]
- PROCTOR, G. R. More additions to the flora of Jamaica. *Jour. Arnold Arb.* 63: 199-315. 1982. [*Argusia*, 294, 295.]
- VALENTINE, D. H. *Argusia*. In: T. G. TUTIN *et al.*, eds., *Fl. Europaea* 3: 84. 1972. [*A. sibirica*.]

5. *Heliotropium* Linnaeus, Sp. Pl. 1: 130. 1753; Gen. Pl. ed. 5. 63. 1754.

Annual or perennial herbs [sometimes subshrubs or shrubs], glabrous or variously pubescent with simple, eglandular trichomes that are rarely mixed with glandular [rarely malpighiaceus] ones. Leaves alternate [rarely opposite or whorled], petiolate or sessile, entire to repand [rarely crenate or dentate]. Inflorescences ebracteate or bracteate, terminal or axillary, single or clustered, dense or lax scorpioid cymes [sometimes reduced to a single flower]; bracts (when present) large or small, leafy [or scalelike]; flowers pedicellate or sessile. Calyx persistent [or rarely caducous], divided almost to base, the lobes green, unequal in length and/or width, linear to lanceolate or ovate, imbricate, erect or spreading to reflexed in fruiting material, variously pubescent or rarely glabrous. Corolla salverform or funnelform, rarely tubular or urceolate, purple or white, with or without a yellow center, sometimes yellow [yellowish green or blue]; tubes pubescent on the outside, rarely glabrous, the throat frequently pubescent, without scales or appendages; limb obscurely to conspicuously lobed, sometimes with five teeth alternating with lobes. Stamens 5, included; filaments short to obsolete; anthers linear to ovate, basifixed, usually cordate at base, free or coherent at the glabrous or pubescent apex. Ovary obscurely lobed or not lobed, 4 loculate, with 1 ovule in each locule; style terminal, short to obsolete, very rarely conspicuous and longer than the ovary; stigmatic apparatus disklike, conical or subulate, the receptive area narrow, ringlike, surrounding the widest lower portion, the remainder of the apparatus sterile, included or exerted, short or extended into a long beak, entire or conspicuously bidentate at apex, glabrous or puberulent to pubescent. Fruit dry, rounded or compressed, obscurely 2 or 4 lobed, glabrous or variously pubescent, smooth or variously sculptured, splitting at maturity into 4 one-seeded nutlets or into 2 one-seeded nutlets [rarely not splitting and consisting of only a one-seeded nutlet]. Seeds usually finely reticulate; embryo curved, cotyledons flat; endosperm forming a thin layer; germination epigeal. Base chromosome numbers 7-9, 11-13, 25. (Including *Batshia* Raf., non J. F. Gmelin (1791), non Mutis ex Thurnberg (1792), non Moench (1794); *Bucanion* Stev.; *Cochranea* Miers; *Euploca* Nutt.; *Heliophytum* (Cham.) A. DC.; *Hieranthemum* (Endl.) Spach; *Lithococca* Small ex Rydb.; *Meladendron* Molina; *Notonerium* Benth; *Orthostachys* (R. Br.) Spach; *Pioctonon* Raf.; *Piptoclaina* G. Don; *Preslaea* Martius; *Sarcanthus* Andersson, non Lindley; *Schleidenia* Endl.; *Schobera* Scop.; *Synzistachium* Raf.; *Tiaridium* Lehm.; *Valentina* Speg., non Hedwig; *Valentinella* Speg.) LECTOTYPE SPECIES: *H. europaeum* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. 3: 73. 1913; Johnston, Contr. Gray Herb. 81: 3. 1928. (Name from Greek *helios*, the sun, and *trope*, a turn; ancient writers believed that the flowers of various members of the genus turned toward the sun.) — HELIOTROPE, TURNSOLE.

A well-defined genus, the second largest of the Boraginaceae, with some 260 species distributed primarily in the drier, temperate and tropical areas of both hemispheres. The centers of greatest diversity are the Irano-Turanian region (Asia) and South America, each of which has about 80 indigenous species. The genus is somewhat poorly developed in Australia (about 25 indigenous species), the Soviet Union (about 25 species) and Europe (10 species). *Heliotropium* is represented in the southeastern United States by ten species, seven of which are indigenous.

The infrageneric classification of *Heliotropium* has not been adequately established on a worldwide basis, although Johnston (1928) and Riedl (1967) have dealt respectively with the South American and central and western Asian sections. Of the slightly more than 20 sections recognized in *Heliotropium*, nearly half are primarily South American. Riedl (1967) subdivided the genus into three subgenera, but it is not necessary to evaluate those critically at this time. Johnston (1928) and Frohlich (1978) are followed here in assigning to sections the species of *Heliotropium* in the Southeastern States.

Section HELIOTROPIUM (sects. *Agoraea* Bunge, *Bucanion* (Stev.) Szegl., *Euheliotropium* Griseb.) (annual herbs, calyx persistent, corolla lobes imbricate in bud, nutlets deciduous), an exclusively Eurasian group, is represented in the Southeast by the weedy, naturalized *Heliotropium europaeum* L. (*H. commutatum* Roemer & Schultes, *H. incandescens* Andrz.), $2n = 24, 32, 48$. This Mediterranean, central European, and southwestern Asian weed is sporadically naturalized in eastern North America, where it grows in waste places and along roadsides. It is easily distinguished from other species of the Southeastern States by its elliptic to ovate, petiolate leaves with rounded to cuneate base; white, sessile flowers; ebracteate helicoid cymes; persistent, star-shaped calyx in fruit; subulate-conical stigma; and four, usually pubescent, tuberculate, readily deciduous, one-seeded nutlets.

Heliotropium europaeum has been recorded from all the Southeastern States except South Carolina and Mississippi, where it is likely to be found. However, all of the reports from Florida (e.g., Fernald; Hommersand; Johnston *et al.*; Small, 1933) apparently were based on a single collection (*Curtiss 6864*, GH!) from a population that did not persist (Ward & Fantz). The species was also collected on ballast in Georgia (*Harper 1526*, GH!), but there, too, it was unsuccessful, and Jones & Coile did not report it for that state.

The well-defined sect. SCHOBERA (Scop.) I. M. Johnston (*Schobera* Scop., *Synzistachium* Raf.) (annual or perennial herbs; calyx persistent, corolla throat densely pubescent; nutlets two, two seeded, compressed, deciduous, covered with obtuse, vesicular appendages) is monotypic. It is based on *Heliotropium angiospermum* Murray (*H. parviflorum* L., *Schobera angiosperma* (Murray) Murray ex Scop., *H. humile* Lam.; see Johnston (1928) for 12 additional synonyms), scorpion tail, $2n = 26$, which grows on sandy, moist bottoms, shell mounds and coastal dunes, in thickets, hammocks, open fields, disturbed ground,

citrus groves, and along roadsides and saline shores. It is a tropical American weed that is widely distributed from northern Chile and Bolivia northward through Central America, the West Indies, and into Mexico, southern Texas, and Florida. It is restricted in the Southeast to Florida, where it is common in the Keys and along the Atlantic coast north to Volusia County and along the Gulf coast to Tampa Bay (Ward & Fantz).

Heliotropium angiospermum is readily distinguished by having petiolate leaves; long, ebracteate inflorescences; sessile white flowers with obsolete styles; and two warty, subdidymous, two-seeded nutlets that are conspicuously covered with vesicular, epidermal appendages.

The monotypic sect. HALMYROPHILA I. M. Johnston (perennial, succulent, glabrous plants; inflorescences ebracteate, the flowers subsessile to short pedicelled; stigma sessile, saucer shaped; fruit splitting at maturity into four glabrous, one-seeded nutlets) comprises the most widely distributed and perhaps one of the most highly variable species in the genus, *Heliotropium curassavicum* L. (*H. angustifolium* Raf., *H. glaucum* Salisb., *H. glaucophyllum* Moench, *H. xerophyllum* Cockerell), seaside heliotrope, $2n = 26, 52$. It is a prostrate to decumbent or rarely erect, somewhat glaucous, succulent perennial that has linear to oblanceolate or spatulate leaves, ebracteate scorpioid cymes, and corky fruits that separate into four one-seeded nutlets. It is highly variable in morphology of leaves, size of corolla limb, and development of the stigmatic column. The species is differentiated into at least five morphologically and somewhat ecogeographically defined entities that have been recognized by various authors as species, subspecies, or varieties. However, the morphological divergence between these is small, and they are best recognized as varieties, two of which, vars. *obovatum* DC. and *oculatum* (Heller) I. M. Johnston ex Tidestrom, are widely distributed in the Southwestern, Mountain and Pacific states and do not reach the Southeast. Two others, vars. *argentinum* I. M. Johnston and *fruticulosum* I. M. Johnston, are exclusively South American, while the fifth, var. *curassavicum*, is by far the most widespread. It is distributed from New Jersey south through all the Southeastern States except Tennessee, Mexico, Central America, the West Indies, and South America into Chile and Argentina. It has become naturalized in Europe, Africa, Asia, and Australia, particularly along the sea shores. Variety *curassavicum* occupies diverse habitats, but in the Southeast it grows primarily in sandy or saline soil, frequently just above the high tide line, along the shores of the Atlantic Ocean and the Gulf of Mexico, as well as in salt marshes, saline flats, edges of mangrove swamps and hammocks, and inland in plains and meadows. It is distinguished from the other varieties by its small, white, yellow-centered corollas (1–2.5 mm long), and from the other taxa of the genus in the Southeast by being completely glabrous.

Section HELIOPHYTUM (Cham.) Griseb. (inflorescence ebracteate; corolla throat and tube villous within; fruit separating at maturity into



FIGURE 3. *Heliotropium*. a-f, *H. curassavicum*: a, flowering shoot, $\times 1/2$; b, portion of inflorescence, $\times 3$; c, flower, $\times 6$; d, gynoecium, $\times 20$; e, fruit, $\times 6$; f, mericarp, adaxial surface, $\times 12$. g-k, *H. polyphyllum*: g, tip of flowering shoot, $\times 1$; h, flower, $\times 6$; i, flower bud just before anthesis, showing imbrication and unequal calyx lobes, $\times 6$; j, same as "i" with one side removed to show relationship of stamens to style, invaginations of corolla, and imbrication of corolla lobes, $\times 12$; k, gynoecium, $\times 15$. l, m, *H. indicum*: l, gynoecium, $\times 15$; m, fruit, $\times 6$. n, *H. tenellum*: gynoecium, $\times 20$.

two two-seeded nutlets, each with a few seedless locules) is almost exclusively South American and contains four species that are distributed east of the Andes. One, *Heliotropium amplexicaule* Vahl (*H. anchusaefolium* Poir., *Cochranea anchusaefolia* (Poir.) Gürke; see Johnston (1928) for 17 additional synonyms), wild heliotrope, $2n =$

26, 28, is cultivated and widely naturalized in the eastern, central, and southern United States and in portions of Australia and Mediterranean Europe. It has been reported from all the Southeastern States except Arkansas. Sharp *et al.* indicated that the plant is an escape in Knox County, Tennessee. It grows in waste places, fields, and disturbed areas, on sandhills, and along roadsides and railroad tracks. *Heliotropium amplexicaule* is easily distinguished by its sessile, repand to crenulate leaves; densely flowered clusters of two to five scorpioid cymes; blue to purple or rarely white, funnellform corollas to 8 mm long; two two-seeded nutlets; and a dense cover of long, spreading trichomes mixed with short, glandular ones. It is the only *Heliotropium* species in the Southeast with glandular trichomes.

Section TIARIDIUM (Lehm.) Griseb. (*Tiaridium* Lehm., *Hieranthemum* (Endl.) Spach) (coarse, weedy annuals; inflorescence ebracteate; corolla funnellform, glabrous within; fruit dividing into two two-seeded, strongly ribbed, bidentate nutlets) includes two South American species, one of which, *Heliotropium elongatum* Hoffm. ex Roemer & Schultes, is restricted to South America and the other a cosmopolitan weed. *Heliotropium indicum* L. (*Tiaridium indicum* (L.) Lehm.; see Johnston (1928) for six additional synonyms), turnsole, $2n = 22$, is readily recognized by its coarsely ovate, long-petiolate leaves; its long, ebracteate inflorescences; its funnellform, light purple, white- or yellow-centered corolla; and its glabrous, smooth, strongly ribbed, divergently four-toothed fruits that split at maturity into two two-seeded nutlets. It is common in all nine states of the Southeast, as well as elsewhere in the eastern, central, and southern United States, in Mexico, Central America, the West Indies, and throughout much of the Old World. It is a weed in almost all tropical and subtropical countries of both hemispheres.

Various authors (e.g., Fernald; Britton & Brown; Small, 1933) have indicated that *Heliotropium indicum* is naturalized from Asia or India. As argued by Johnston (1928), however, the species is most likely South American, is unrelated to any of the Asiatic members of the genus, and is most closely related to the South American *H. elongatum*, from which it differs only in the size, divergence, and apex of the nutlets.

The remaining five species of *Heliotropium* that grow in the southeastern United States belong to sect. ORTHOSTACHYS (inflorescence bracteate or ebracteate; anthers ovate to linear, glandular or pubescent at the frequently coherent apex; style well developed; fruit splitting at maturity into four one-seeded nutlets, the inner face of each nutlet often marked by an elliptical or circular pit). This section, the largest in the genus, includes more than 130 species. Johnston (1928) recognized three reasonably well-defined subsections. In contrast Riedl (1967) raised the section to subgeneric rank and treated one of its subsections as a section.

Two of the subsections of sect. ORTHOSTACHYS are present in the Southeast. The third, subsect. *Axillaria* I. M. Johnston (flowers from the axils of large, leaflike bracts), is exclusively Mexican and South

American. Subsection *Ebracteata* I. M. Johnston (inflorescence an ebracteate, scorpioid cyme) is represented in our area by *Heliotropium procumbens* Miller (*H. americanum* Miller, *H. inundatum* Sw., *H. rigidulum* DC.), $2n = 14, 28$, which is distributed in Florida, Mississippi, Louisiana, and Arkansas, west through Texas to California, south into Mexico, Central America, the West Indies, and South America into northern Argentina. The record from Arkansas is based on *Demaree* 26535 (GH), from Desha County. *Heliotropium procumbens* is easily distinguished from the other heliotropes of the Southeast in having short-petiolate, narrowly oblanceolate to elliptic leaves; ebracteate, scorpioid cymes clustered in groups of two to five; white corolla 1.5–3 mm long; sessile stigma; and four-lobed, globose fruits that split at maturity into four one-seeded nutlets that are rounded, strigose to hispidulous on the back, and angled, smooth, not pitted on the inner face. It is a weedy plant that usually grows on damp alluvial soil in flood plains, pinelands, mud flats, waste land, fields, and coastal hammocks.

Section ORTHOSTACHYS subsect. *Bracteata* I. M. Johnston (inflorescence a scorpioid, bracteate cyme), which is taxonomically the most difficult group in the genus because its species are very variable and poorly defined (Johnston, 1928), includes four species in our area. *Heliotropium convolvulaceum* (Nutt.) Gray (*Euploca convolvulacea* Nutt., *Batschia albiflora* Raf., *E. albiflora* (Raf.) I. M. Johnston, *E. aurea* Rose & Standley), $2n = 42$, is distributed primarily in the western United States and northern Mexico. Its range extends from Wyoming east into Nebraska, south into central Arkansas (Jefferson and Pulaski counties; see E. B. Smith), and all the other Southeastern States, and northern Mexico (Sonora and Chihuahua; Frolich, 1978), and west into Nevada, Utah, and California (Cronquist, 1984). *Heliotropium convolvulaceum* is a densely strigose annual, with stiff, appressed trichomes; short-petiolate, lanceolate to ovate leaves; white, widely funnelform, almost unlobed corollas 15–22 mm long and conspicuously plicate in bud; a slender style 3–4 mm long topped by a truncate stigmatic appendage with a penicillate cluster of hairs; and a two-lobed fruit that splits into four one-seeded nutlets, each with an asymmetric, convex, silky abaxial side and two, unequal, glabrous commissural faces, the smaller one bearing a pit. Johnston (1932) recognized California plants of this species, which have spreading trichomes, as var. *californicum* (Greene) I. M. Johnston.

The nearest relative of *Heliotropium convolvulaceum* is *H. racemosum* (Rose & Standley) I. M. Johnston, which is endemic to the Coastal Plain of southern Texas and the area southeast of San Antonio. It has smaller flowers, a star-shaped corolla with acute lobes, and denser inflorescences.

Heliotropium tenellum (Nutt.) Torrey (*Lithospermum tenellum* Nutt., *Lithococca tennella* (Nutt.) Small, *H. Nuttallii* House) grows primarily on limestone in cedar glades, on rocky or gravelly calcareous prairies, or on dolomite soil of open areas. It occurs from Kentucky,

Missouri, and Kansas south into Tennessee (Rutherford and Wilson counties), Georgia (Catoosa County), Alabama (widespread), Mississippi (Oktibbeha County), Arkansas (widespread), Oklahoma, Texas, and northern Mexico (Coahuila) (Frohlich, 1978). It is a slender, annual herb, grayish strigose with appressed trichomes; revolute-margined, linear leaves to 5 cm long and 4 mm wide; loose, bracteate, raceme-like cymose inflorescences; conspicuously pedicellate flowers; extremely unequal, foliaceous, linear calyx lobes; and subspherical, finely pubescent fruits that spit into four one-seeded nutlets. The revolute leaf margins and dense cover of appressed trichomes reduce the rate of transpiration and maintain leaf temperatures close to those of the surrounding air (2.5° above to 3° below) enabling the plant to endure the summer drought and high temperatures of the glades in which it most frequently grows (Baskin & Baskin).

Heliotropium fruticosum L. (*H. campechianum* HBK., *H. phyllostachyum* Torrey, *H. phyllostachyum* var. *erectum* Macbr., *H. asurgens* I. M. Johnston, *H. texanum* I. M. Johnston, *Anchusa incana* Sessé & Moc.), $2n = 42$, is distributed from Texas south through Mexico, Central America, and northern South America. In the southeastern United States, it is known only from the Florida Keys: Key West (older collections only) and Sugarloaf Key (Ward & Fantz).

Heliotropium polyphyllum Lehm. (*H. polyphyllum* var. *Leavenworthii* A. Gray, *H. Leavenworthii* (A. Gray) Small, *H. horizontale* Small, *H. polyphyllum* var. *horizontale* (Small) R. W. Long) grows in hammocks, wet pinelands, cypress and marl prairies, and waste ground, on sand dunes, and along roadsides and brackish shores. Its distribution includes South America, the Bahamas, and southern Florida, with extensions northward along the Atlantic coast to Volusia County and along the Gulf coast to Taylor County (Ward & Fantz).

Both *Heliotropium fruticosum* and *H. polyphyllum* have linear to lanceolate, short-petiolate, strigose leaves with appressed trichomes, white or yellow corollas with a pubescent throat, bracteate inflorescences, and strigose fruits that split at maturity into four one-seeded nutlets. *Heliotropium fruticosum* is an annual, with usually revolute leaf margins, subequal calyx lobes 1–2.5 mm long, and cymose inflorescences of small flowers that are twice as numerous as the bracts. In contrast, *H. polyphyllum* is a perennial with flat leaves, conspicuously unequal calyx lobes (2.5–)3–6.5 mm long, and inflorescences with larger flowers that are nearly as many as the bracts.

Heliotropium polyphyllum is highly variable in habit and flower color. Forms with erect or prostrate stems and yellow, white, or yellow-centered white flowers have been recognized variously as species or varieties (Long; Ward & Fantz; Small, 1903, 1933). Johnston (1928) wrote (p. 64) that "*H. Leavenworthii* Torrey and *H. horizontale* Small from Florida all represent northern forms of *H. polyphyllum*" and that "they will eventually be treated as varieties of that species." Johnston's view in treating the Florida plants as "forms" of *H. polyphyllum* seems appropriate, but the recognition of any of these minor variants at the

varietal rank does not. Many of the earlier workers, including Johnston (1928), credited *H. Leavenworthii* to Torrey. However, this name was never published by Torrey and was first recognized at the specific rank by Small (1903). The correct citation of this name at that level should be *H. Leavenworthii* (A. Gray) Small.

Heliotropium is characterized in subfamily Heliotropioideae by its mainly herbaceous habit, dry fruits that split at maturity into four one-seeded nutlets or two two-seeded ones, and conical to discoid stigmatic apparatus with the receptive area restricted to a narrow rim at the widest part of the lower portion. The monotypic genus *Nogalia* Verdcourt (southern Arabia and Somalia) has stigmas similar to *Heliotropium* but differs markedly in the fruit structure (Verdcourt).

The reproductive biology of *Heliotropium* is poorly studied, and little has been added about the pollinators since Knuth's treatment of *H. europaeum* and *H. arborescens* L. (as *H. peruvianum* L.) The genus is highly diversified in size, color, and scent of flowers; in the nature of the pubescence of the corolla throat; in size, insertion and coherence of anthers; and in the shape and complexity of the stigmatic apparatus. However, hardly anything is known about the adaptive significance of this diversity in relation to specific pollinators. Frohlich (1978) reported functional dioecy in *H. fallax* I. M. Johnston (Baja California south into Guatemala) and stated that the staminate plants rarely set fruit, whereas the carpellate ones have variable, often low fruit set.

The positioning of the flowers close to the leaves was shown by Frohlich (1976) to have an interesting ultraviolet (UV) pattern. The glaucous foliage, sepals, and stems of *Heliotropium curassavicum* and the densely pubescent plant parts of other species reflect ultraviolet (UV) light, while the upper corolla surface absorbs it. Furthermore, in *H. ternatum* Vahl the trichomes on the folded tips and back of the corolla lobes reflect UV light, and the expanded hairless portions absorb it. He also observed that only the silicified trichomes have UV reflectance, whereas the rigid, trichome-shaped, unsilicified elongations from the upper epidermis of the corolla are UV absorbing.

Chromosome numbers have been reported for more than forty species (about 14 percent) of *Heliotropium* (my compilation). Aneuploidy occurs in certain species, such as *H. amplexicaule* ($n = 13, 14$), *H. curassavicum* ($n = 12, 13$), and *H. indicum* ($n = 11, 12$). In *H. curassavicum* diploids and tetraploids based on 13 have been reported for various varieties (Frohlich, 1980). Most reports are based on single counts, and the extent of variation in chromosome numbers within most species is not known. Polyploidy is apparently widespread in the genus. Frohlich (1978) suggested that sect. *Orthostachys* subsect. *Ebracteata* has a base number of seven, whereas subsect. *Bracteata* is based on seven, eight, and secondarily thirteen. Many more counts are needed, however, before any generalizations can be made. On the basis of the formation of univalents and multivalents at meiosis, Faruqi

(1961a) suggested that *H. variflorum* Stocks is a segmental allopolyploid. Neither experimental evidence for this nor putative parents were given.

Markova & Ivanova (1971) observed that the karyotype of *Heliotropium europaeum*, $2n = 48$, consists of five metacentric pairs of chromosomes, 18 submetacentric pairs, of which one has satellites, and one acrocentric pair. The karyotype of *H. indicum*, $2n = 22$, is made up of three pairs of short metacentric chromosomes, five short to medium-sized submetacentric pairs, one medium-sized metacentric pair, and two long metacentric pairs, one pair of which has satellites (Bhattacharya). The karyotypes of the other species have not yet been studied.

Because of their potential medicinal value and their poisonous effect on humans and animals, pyrrolizidine alkaloids of *Heliotropium* have been more extensively surveyed than any other class of natural products. At least 45 species have been surveyed; all appear to contain unsaturated pyrrolizidines, and some contain saturated ones as well. Although some of the distributional patterns of these compounds are useful in distinguishing between some closely related species, geographical differentiation in the pyrrolizidine profiles within species (e.g., *H. curassavicum*) has been found. It has been concluded that the necine patterns do not appear to provide evidence of species relationships (Birecka, Frohlich, & Glickman).

Poisoning of domestic animals by pyrrolizidine alkaloids from *Heliotropium* and other plants has long been suspected, but only recently has experimental work provided solid evidence of that (Bull *et al.*). These alkaloids have been reported to have antimitotic, carcinogenic, hemolytic, hepatotoxic, mutagenic, and pulmotoxic effects in domestic and experimental animals. Of these compounds, heliotrine and lasiocarpine, both widespread in *Heliotropium*, are the most active principles (for references, see Birecka, Frohlich, Hull, & Chaskes).

The most common type of pollen in *Heliotropium* is subprolate and 3-colporate, with three main colpi alternating with three pseudocolpi (Frohlich, 1978; Nowicke & Skvarla, ref. in *Tournefortia*). Pollen sculpturing varies from psilate to faintly rugulate, punctate, to scabrate (Quiroz-García & Palacios-Chávez). Tetracolporate pollen without additional pseudocolpi was also found. In *H. convolvulaceum* 6- or 7-porate grains have been reported by Frohlich (1978), whereas the 8-colporate type was observed by Clarke. The scant data do not allow meaningful conclusions about a correlation between palynology and the infrageneric classification of *Heliotropium*. It appears, however, that palynology might be a useful approach.

Frohlich (1978) found that the organization of the foliar photosynthetic tissue of *Heliotropium* falls basically into two well-defined types, kranz and non-kranz. In the kranz type, in which the C_4 pathway of carbon fixation is used, the bundle sheath consists of thick-walled cells with numerous chloroplasts, and the mesophyll, which has fewer chloroplasts, is organized radially around the sheath and is not differentiated into palisade and spongy chlorenchyma. The kranz organization occurs

in members of sect. *Orthostachys* subsects. *Bracteata* and *Axillaria*. The non-kranz type, which was found in all the Mexican members of subsect. *Ebracteata*, uses the C_3 pathway of carbon fixation. Leaf anatomy in this subsection shows that the bundle sheath either contains some chloroplasts or has none, and the mesophyll is well organized into palisade and spongy chlorenchyma that are not organized radially around the sheath.

Nutlet dispersal has been observed for *Heliotropium curassavicum* and *H. indicum* (Ridley). The former was said to be transported in crevices in pumice and in holes in drifting logs. However, Johnston (1959) stated that the corky mesocarp of *H. curassavicum* aids in the dispersal of nutlets by water. Ridley indicated that *H. indicum* is dispersed in the Northern Hemisphere by the gadwall, a duck of the genus *Chaulelasmus*.

The physiological ecology of *Heliotropium curassavicum* has been studied in some detail by Mooney and Roy & Mooney (1982, 1987). They discovered that plants of this species from cool, maritime areas have a photosynthetic acclimation potential higher than those of desert habitats, that both have similar stomatal conductance, but the desert plants showed plastic response to dry-air growing conditions, and that the desert plants are taller and with smaller, thinner leaves than the coastal plants.

Heliotropium arborescens is extensively cultivated for the perfume industry, as well as an ornamental, for its purple, highly fragrant flowers (Graf; Hill). *Heliotropium amplexicaule* and *H. curassavicum* are also widely cultivated as ornamentals (Brummitt, 1972; Riedl, 1978).

Many species of *Heliotropium* are noxious weeds that are toxic to domestic animals (Everist; Kingsbury). Numerous cases of cattle, sheep, and horse mortality have resulted from feeding on plants of this genus. As noted above, it has been shown that pyrrolizidine alkaloids are the poisonous principles. Numerous medicinal values have been attributed to various species of *Heliotropium* (see H. M. Burkill, Duke & Ayensu, Hartwell, Perry, and Uphof). Extracts from certain species have shown significant antitumor activity against certain types of leukemia and melanoma.

REFERENCES:

- Under family references see ADAMS; AL-NOWAIHI *et al.*; ALTAMURA *et al.*; AYENSU; BAILEY; BAILLON, BELL & TAYLOR; BENTHAM & HOOKER; BHATTACHARYA; BOL-KHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; H. M. BURKILL; I. H. BURKILL; DE CANDOLLE; CHAPMAN; G. C. S. CLARKE; CLEWELL; CORRELL & CORRELL (1972, 1978); CORRELL & JOHNSTON; DEAN *et al.*; DíEZ (1984); DUKE & AYENSU; DUNCAN & FOOTE; DUNCAN & KARTESZ; EVERIST; FABRE; FERNALD; FERNANDES & LEITÃO; GATTINGER; GLEASON; GODFREY & WOOTEN; GOLDBLATT (1981, 1984, 1985, 1988); GRAF; GUNN *et al.*; GUPTA; HEGI; HIGGINS (1979); HILL; HOMMERSAND; HOWARD; HUNTER; JODIN; JOHNSTON (1928, 1932, 1935a, 1936, 1937, 1951a, 1959); JOHNSTON *et al.*; JONES & COILE; KINGSBURY; KLEIMAN *et al.*; KNUTH; LAKELA & CRAIGHEAD; LEWIS & ELVIN-LEWIS;

LIOGIER; LONG & LAKELA; MACROBERTS; MARKOVA & IVANOVA (1971); MARTICORENA; MARTINS; J. S. MILLER; R. B. MILLER; MITCHELL & ROOK; MOERMAN; MOHR; R. J. MOORE (1973, 1974, 1977); MUENSCHER; MÜLLER; NOWICKE; ORNDUFF (1967, 1968, 1969); PARK; PATEL *et al.*; PERRY; POLLARD & AMUTI; POPOV (1953); QUISUMBING; RICKETT; RIDLEY; RIEDL (1967); SATYAVATHI & NARAYANA; SHARP *et al.*; SINGH; SMALL (1903, 1913, 1933); E. B. SMITH; L. B. SMITH; SMITH & CULVENOR; STANDLEY; STEYERMARK; SYNGE; TÉTÉNYI; UPHOF; VERDCOURT; WARD & FANTZ; WIGGINS (1971); WILLAMAN & LI; WILLAMAN & SCHUBERT; WUNDERLIN; and ZALKOW *et al.*

AMLADI, S. R. Danaid butterflies attracted to *Heliotropium indicum* (Boraginaceae), an alkaloid containing plant. Jour. Bombay Nat. Hist. Soc. **72**: 585-587. pl. 1975. [Butterflies feeding on decaying inflorescences.]

ATCHUTA-RAMAMURTI, B. Life history of *Heliotropium curassavicum* Linn. Jour. Vikram Univ. **2**: 134-137. 1958.*

BAQUAR, S. R., & S. A. HUSAIN. Chromosome studies in some flowering plants of West Pakistan. I. Phytot Argentina **24**: 49-55. 1967. [*H. europaeum*, *H. subulatum*, 54.]

BABALONAS, D. Zwei in Griechenland eingeschleppte amerikanische Pflanzenarten: *Cenchrus pauciflorus* und *Heliotropium curassavicum*. (English and Greek summaries.) Ann. Mus. Goulandris **3**: 19-22. 1977. [First record of *H. curassavicum* from Greece.]

BASKIN, J. M., & C. C. BASKIN. Leaf temperatures of *Heliotropium tenellum* and their ecological implications. Am. Midl. Nat. **100**: 488-492. 1978. [Plants maintain leaf temperatures near those of the air; physiological values of such adaptation.]

BHATIA, R. C. Seed variability in *Heliotropium supinum*. Geobios **8**: 112-115. 1981.*

———. Foliar epidermal studies of *Heliotropium supinum* L. Folia Geobot. Phytotax. **19**: 381-385. 1984. [Frequencies and distributions of trichomes and stomata.]

BIRECKA, H., T. E. DiNOLFO, W. B. MARTIN, & M. W. FROHLICH. Polyamines and leaf senescence in pyrrolizidine alkaloid-bearing *Heliotropium* plants. Phytochemistry **23**: 991-997. 1984. [*H. angiospermum*, *H. indicum*.]

———, M. W. FROHLICH, & L. M. GLICKMAN. Free and esterified necines in *Heliotropium* species from Mexico and Texas. *Ibid.* **22**: 1167-1171. 1983. [Fourteen species analyzed.]

———, L. HULL, & M. J. CHASKES. Pyrrolizidine alkaloids of *Heliotropium* from Mexico and adjacent U.S.A. *Ibid.* **19**: 421-426. 1980. [Twenty-four species of *Heliotropium*; greenhouse plants have significantly higher concentrations than their corresponding field samples.]

BOPPRE, M. Adult Lepidoptera "feeding" at withered *Heliotropium* plants (Boraginaceae) in East Africa. Ecol. Entomol. **6**: 449-452. 1981. [Twenty-seven species of moths and butterflies of families Arctiidae, Ctenuchidae, and Danaidae attracted to *Heliotropium*.]

BULL, L. B., E. S. ROGERS, J. C. KEAST, & A. T. DICK. *Heliotropium* poisoning in cattle. Austral. Vet. Jour. **37**: 37-43. 1961.*

BUNGE, A. VON. Über die *Heliotropien* mitelländisch-orientalischen Flora. Bull. Soc. Nat. Moscou **42**: 279-332. 1870. [Seventy species in 11 sections; keys to sections and to species.]

BURTT, B. L. *Heliotropium persicum* and *H. undulatum*. Kew Bull. **4**: 137, 138. 1949. [Nomenclature; *H. bacciferum*, *H. ramoissimum*, *Sericostoma*.]

———. Inland occurrence of *Heliotropium curassavicum*. Notes Bot. Gard. Edinburgh **26**: 357. 1966. [In Pakistan.]

- BRUMMITT, R. K. The diagnostic characters of the European *Heliotropium* species. Bot. Jour. Linn. Soc. **64**: 60-67. 1971. [Evaluation of taxonomic characters and of taxa.]
- . *Heliotropium*. In: T. G. TUTIN *et al.*, eds., Fl. Europaea **3**: 84-86. 1972. [Twelve species recognized.]
- CATALFAMO, J. L., M. W. FROHLICH, W. B. MARTIN, JR., & H. BIRECKA. Necines of alkaloids in *Heliotropium* species from Mexico and the U.S.A. Phytochemistry **21**: 2677-2682. 1982. [Twenty species; necine pattern differs significantly from that of Asian species.]
- , W. B. MARTIN, JR., & H. BIRECKA. Accumulation of alkaloids and their necines in *Heliotropium curassavicum*, *Heliotropium spathulatum*, and *Heliotropium indicum*. *Ibid.* **21**: 2669-2675. 1982.
- , ———, M. W. FROHLICH, & H. BIRECKA. Pyrrolizidines in species of *Heliotropium*. (Abstract.) Pl. Physiol. **67** (Suppl.): 112. 1981. [*H. curassavicum*, *H. indicum*, *H. spathulatum*.]
- CHAUDHARY, S. A. Studies on *Heliotropium* in Saudi Arabia. Arab. Gulf Jour. Sci. Res. **3**: 33-53. 1985.*
- CRAVEN, L. A. *Heliotropium*. In: J. P. JESSOP & H. R. TOELKEN, eds., Fl. So. Australia. ed. 4. **3**: 1162-1166. 1986. [Nine species; incl. *H. amplexicaule*, *H. curassavicum*, and *H. europaeum*.]
- CRISP, M. D. *Notonerieum* (Apocynaceae) laid to rest in the Boraginaceae. Jour. Adelaide Bot. Gard. **6**: 189-191. 1983. [A species of *Heliotropium* endemic to Australia.]
- CROWLEY, H. C., & C. C. J. CULVENOR. The alkaloids of *Heliotropium supinum* L., with observations on viridifloric acid. Austral. Jour. Chem. **12**: 694-705. 1959. [Supinine, heliosupinine, and echinatine as the major components.]
- CULVENOR, C. C. J. Herbs, health and *Heliotropium*. Food Technol. Austral. **39**: 387, 388. 1987.*
- , L. J. DRUMMOND, & J. R. PRICE. The alkaloids of *Heliotropium europaeum*. I. Heliotrine and lasiocarpine. Austral. Jour. Chem. **7**: 279-286. 1954. [Part II. *Ibid.* 287-297.]
- CUSICK, A. W. A new West Virginia borage. Castanea **32**: 192. 1967. [*H. tenellum* in Mason County.]
- DATTAGUPTA, S., & P. C. DATTA. Pharmacognostic study of the leaf of *Heliotropium indicum* Linn. (Boraginaceae). Quart. Jour. Crude Drug Res. **15**: 141-151. 1977. [Medicinal value; leaf anatomy, trichome types; chemical constituents.]
- DAVICINO, J. G., M. J. PESTCHANKER, & O. S. GIORDANO. Pyrrolizidine alkaloids from *Heliotropium curassavicum*. Phytochemistry **27**: 960-962. 1988. [Vars. *argentinum* and *curassavicum*.]
- DI FULVIO, T. E. Recuentos cromosómicos en *Heliotropium* (Boraginaceae). (English summary.) Kurtziana **5**: 89-95. 1969. [Counts for 12 species.]
- EWAN, J. A review of the North American weedy heliotropes. Bull. So. Cal. Acad. Sci. **41**: 51-57. 1942. [*H. curassavicum* recognized as two species with two subspecies each.]
- FARUQI, S. A. Cytological studies in *Heliotropium* from West Pakistan. Caryologia **14**: 313-318. 1961a. [Chromosome counts for seven species.]
- . A cytological note on *Heliotropium angiospermum* Murray. Southwest. Nat. **6**: 100. 1961b. [*n* = 13.]
- . Abnormal meiosis and polyad formation in *Heliotropium ophioglossum*. Cytologia **26**: 182-187. 1961c.
- & I. V. HOLT. Studies of teratology in *Heliotropium curassavicum* L. Proc. Okla. Acad. Sci. **41**: 19-22. 1960 [1961d].*

- FROHLICH, M. W. Appearance of vegetation in ultraviolet light: absorbing flowers, reflecting backgrounds. *Science* **194**: 839-841. 1976. [Appearance of inflorescences of *H. calcicola*, *H. curassavicum*, and *H. ternatum* in ultraviolet and in visible light.]
- . Systematics of *Heliotropium* section *Orthostachys* in Mexico. 277 pp. type-script. Unpubl. Ph.D. dissertation, Harvard Univ. 1978. [Treatment of 22 species; morphology, anatomy, cytology, seed set, taxonomy.]
- . In: Chromosome number reports LXIX. *Taxon* **29**: 703-730. 1980. [P. 705, *H. curassavicum* var. *curassavicum*, $2n = 52$; *H. curassavicum* var. *oculatum*, $2n = 26$.]
- . *Heliotropium*. In: D. L. NASH & N. P. MORENO, Boraginaceae. Fl. Veracruz **18**: 70-140. 1981. [Treatment of 14 species, including five of the ten occurring in the southeastern U.S.]
- & P. J. FERRONE. In: Chromosome number reports LXXXIII. *Taxon* **33**: 351-354. 1984. [Counts for seven species of *Heliotropium*, 351.]
- GANGULI, N. Las especies silvestres de *Heliotropium* de la República Argentina. (English summary.) *Revista Facul. Cien. Exac. Fis. Nat.* **17**: 481-560. 1955. [Twenty-three species; morphology, distribution, taxonomy; key, illustrations.]
- HARPER, P. A. W., K. H. WALKER, R. E. KRAHENBUHL, & B. M. CHRISTIE. Pyrrolizidine alkaloid poisoning in calves due to contamination of straw by *Heliotropium europaeum*. *Austral. Vet. Jour.* **62**: 382, 383. 1985.
- HARSHBERGER, J. W. The comparative leaf structure of the sand dune plants of Bermuda. *Proc. Am. Philos. Soc.* **47**: 97-110. pls. 1-3. 1908. [Includes *H. curassavicum*.]
- HILGER, H. H. Fruchtsbiologische Untersuchungen an Heliotropioideae (Boraginaceae). I. Die Ontogenie der monospermen Früchte von *Heliotropium supinum* L. (English summary.) *Flora* **179**: 291-303. 1987. [Development, morphology, and anatomy of the one-seeded fruit.]
- JAIN, S. C., & M. PUROHIT. Antitumor active pyrrolizidine alkaloids from *Heliotropium marifolium* Retz. *Chem. Pharm. Bull. Tokyo* **34**: 5154-5156. 1986.*
- KHALEEL, T. F. Embryology of *Heliotropium scabrum* and *H. strigosum* (Boraginaceae). *Pl. Syst. Evol.* **129**: 45-62. 1978. [Mega- and microsporogenesis, embryogeny, development of pericarp and seed coat.]
- KHALIFA, S. F., & K. A. K. HAMED. Studies on the Boraginaceae. I. Taxonomic trends in selected species of *Heliotropium*. *Ain Shams Univ. Fac. Agr. Res. Bull.* **1960**: 1-15. 1982. [Floral anatomy of *H. arbainense*, *H. bacciferum*, *H. digynum*, *H. europaeum*, and *H. supinum*.]
- KUGELMAN, M., W.-C. LIU, M. AXELROD, T. J. MCBRIDE, & K. V. RAO. Indicine-N-oxide: the antitumor principle of *Heliotropium indicum*. *Lloydia* **39**: 125-128. 1976.
- LÉONARD, J. Contribution à la connaissance de la flore de l'Iran. —VII. Note sur deux *Heliotropium* (Boraginaceae). (English summary.) *Bull. Jard. Bot. Nat. Belg.* **54**: 498-500. 1984. [*H. micranthos*, *H. remotiflorum*.]
- LONG, R. W. Additions and nomenclatural changes in the flora of southern Florida—I. *Rhodora* **72**: 17-46. 1970. [*H. polyphyllum*; key to the varieties, a new combination; 32, 33.]
- MALIK, C. P., S. M. SEHGAL, & S. L. TANDON. Chromosome number in some species of *Heliotropium*. *Curr. Sci. Bangalore* **28**: 500. 1959. [*H. Eichwaldii*, $n = 32$; *H. strigosum*, $n = 13$; *H. undulatum*, $n = 16$.]
- MATTOCKS, A. R., R. SCHOENTAL, H. C. CROWLEY, & C. C. J. CULVENOR. Indicine: the major alkaloid of *Heliotropium indicum* L. *Jour. Chem. Soc.* **1961**: 5400-5403. 1961.
- MCCARTEN, N. Succulent heliotropes. *Cact. Succ. Jour. U.S.A.* **47**: 177. 1975. [*H. curassavicum*.]

- McVAUGH, R., & A. S. DELCOURT. *Antiphytum Parryi* (Boraginaceae) confused with *Heliotropium limbatum*. Contr. Univ. Michigan Herb. 11: 69-71. 1975. [Distribution, distinguishing characters, illustrations, map.]
- MOHARANJ, S., P. KULANTHAIVEL, P. S. SUBRAMANIAN, & W. HERZ. Helifoline, a pyrrolizidine alkaloid from *Heliotropium ovalifolium*. Phytochemistry 20: 1991-1995. 1981.
- , P. S. SUBRAMANIAN, & W. HERZ. Minor alkaloids of *Heliotropium curassavicum*. Ibid. 21: 1775-1779. 1982. [Thirteen alkaloids identified.]
- MOONEY, H. A. Photosynthetic plasticity of populations of *Heliotropium curassavicum* L. originating from differing thermal regimes. Oecologia 45: 372-376. 1980. [Plants of cool, maritime climates have greater acclimation potential than those of desert habitats.]
- MOORE, C. W. E. Observations on the autecology of *Heliotropium europaeum* L. in New South Wales and Victoria. Austral. Commonwealth Sci. & Indus. Res. Organ. Div. Plant Indus. Tech. Paper. 7. 12 pp. 1956.*
- MUNIAN, M. Cytomorphological studies in *Heliotropium*. Proc. Indian Sci. Congr. Assoc. 69: 231. 1982.*
- MURTY, Y. S., & S. AGRAWAL. Floral anatomy of Boraginaceae II. *Heliotropium*. Acta Bot. Indica 15: 280-291. 1987. [Vascular anatomy of eight species placed in four groups; cf. KHALIFA & HAMED.]
- NELSON, P. W. A new halophyte for Missouri. Castanea 44: 246, 247. 1979. [*H. curassavicum*.]
- PAL, P. K. Chromosome number in the genus *Heliotropium* Linn. Curr. Sci. Bangalore 26: 218. 1957. [*H. curassavicum*, $n = 11$, $2n = 22$; *H. ovalifolium*, $n = 16$, $2n = 32$; *H. peruvianum*, $n = 9$, $2n = 18$.]
- . Comparative studies in four species of *Heliotropium* L. Proc. Natl. Inst. Sci. India B. 29: 1-41. 1963.*
- PANDEY, J. V., J. P. SINGH, Y. V. RAO, & S. B. ACHARYA. Isolation and pharmacological action of heliotrine, the major alkaloid of *Heliotropium indicum* seeds. Pl. Medica 45: 229-233. 1982.
- PATTON, J. E., & W. S. JUDD. Vascular flora of Paynes Prairie Basin and Alachua Sink Hammock, Alachua County, Florida. Castanea 51: 88-110. 1986. [*H. amplexicaule*, 100.]
- PÉREZ-MOREAU, R. L. Nota sobre dos *Heliotropium* argentinos (Boraginaceae). Darwiniana 13: 67-71. 1963. [*H. pallescens*, *H. transalpinum*.]
- & E. SANCHEZ. Una especie de *Heliotropium* (Boraginaceae) nueva para la flora argentina. (English summary.) Ibid. 26: 377-380. 1985. [*H. Hasslerianum*; morphology, leaf anatomy; plant has C_4 type photosynthesis.]
- PULLEN, T. M., S. B. JONES, JR., & J. R. WATSON, JR. Additions to the flora of Mississippi. Castanea 33: 326-334. 1968. [*H. tenellum* from Noxubee, Chickasaw, and Oktibbeha counties, 332.]
- QURESHI, U. S. Studies on the pollen morphology of the genus *Heliotropium* L. from Pakistan. Pakistan Jour. Bot. 17: 107-114. 1985. [Twenty species; light microscopy, key to the species based on pollen morphology.]
- QUIROZ-GARCÍA, D. L., & R. PALACIOS-CHÁVEZ. Catálogo palinológico para la flora de Veracruz. No. 27. Familia Boraginaceae, género *Heliotropium*. (English summary.) Biotica 10: 341-358. 1985. [Twelve species; pollen heterocolporate and tri- to pentacolporate; true colpi alternating with two or three pseudocolpi; key to species.]
- RIEDL, H. Die Gattung *Heliotropium* in Europa. (English summary). Ann. Naturhist. Mus. Wien 69: 81-93. 1966. [Seven species; diagnostic characters, distribution; *H. Halacsyi*, sp. nov.]
- . *Heliotropium*. In: P. H. DAVIS, ed., Fl. Turkey 6: 248-255. 1978. [Fourteen species.]

- . *Heliotropium lasianthum* (Boraginaceae), a new endemic species from Iraq. Kew Bull. **33**: 517–520. 1979. [Anomalous in the genus; sectional position and limits.]
- ROY, J., & H. A. MOONEY. Physiological adaptation and plasticity to water stress of coastal and desert populations of *Heliotropium curassavicum* L. Oecologia **52**: 370–375. 1982.
- & ———. Contrasting morphological and physiological traits of *Heliotropium curassavicum* L. plants from desert and coastal populations. Acta Oecol. (Oecol. Pl.) **8**: 99–112. 1987.
- SAHAY, S. K. Pollen morphology of *Heliotropium*. Jour. Palyn. **9**: 167–176. 1973. [Fourteen species, light microscopy.]
- SANKHLA, N. Role of morphactin in inflorescence development of *Heliotropium Eichwaldii*. Zeitschr. Pflanzenphysiol. **63**: 214–216. 1970. [Development of inflorescence was arrested following treatment with morphactine and a single flower was produced instead of a normal cyme.]
- SASTRI, B. N., ed. The wealth of India. Vol. 5. Frontisp. + xxv + 332 pp. 16 pls. + xii. New Delhi. 1959. [*Heliotropium*, 29–31.]
- SCHOENTAL, R., M. E. FOWLER, & A. COADY. Islet cell tumors of the pancreas found in rats given pyrrolizidine alkaloids from *Amsinckia intermedia* Fisch. & Mey. and from *Heliotropium supinum* L. Cancer Res. **30**: 2127–2131. 1970.
- SHARMA, R. Floral anatomy of *Heliotropium indicum* L. Agra Univ. Jour. Res. Sci. **3**: 349–357. 1954.*
- SHAVER, J. M. Some rare plants of Tennessee. Jour. Tenn. Acad. Sci. **32**: 46–54. 1957. [*H. europaeum*, 49, 50, fig. 4.]
- SMALL, J. K. *Heliotropium polyphyllum*. Addisonia **4**: 25, 26. pl. 133. 1919a. [Description, occurrence in Florida.]
- . *Heliotropium Leavenworthii*. Ibid. 29, 30. pl. 135. 1919b. [Description, synonymy, habitat, and occurrence in Florida.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez *l'Heliotropium peruvianum* L. Compt. Rend. Acad. Sci. Paris **217**: 551–553. 1943.
- SURI, O. P., R. S. SAWHNEY, & C. K. ATAL. Pyrrolizidine alkaloids from *Heliotropium Eichwaldii* and *Lindlofia spectabilis*. Indian Jour. Chem. **13**: 505, 506. 1975. [*H. Eichwaldii* contains four alkaloids, including heliotrine and lasiocarpine.]
- VERDCOURT, B. On the typification of *Heliotropium supinum* L. (Boraginaceae). Kew Bull. **42**: 710. 1987.
- ZALKOW, L. H., L. GELBAUM, & E. KEINAN. Isolation of the pyrrolizidine alkaloid europine N-oxide from *Heliotropium maris-morti* and *H. rotundifolium*. Phytochemistry **17**: 172. 1978.

Subfam. IV. BORAGINOIDEAE.

Tribe 1. TRIGONOTIDEAE (Popov) H. Riedl, Fl. Iranica **48**: 53. 1967.6. *Mertensia* Roth, Catal. Bot. **1**: 34. 1797, nom. cons.

Glabrous [strigose, or hirsute] perennial herbs, occasionally glaucous, with somewhat fleshy [or woody], rhizomelike [or cormlike], branched or unbranched caudex. Stems one to several from the base, erect [decumbent or procumbent]. Leaves entire, alternate, glabrous [or pubescent], the lowermost long- [or short-] petiolate, the upper ones subsessile [or petiolate], obtuse [to acuminate], herbaceous [or fleshy], with [or without] prominent lateral veins. Inflorescences small, congested [or lax],

ebracteate, unilateral, scorpioid cymes, usually elongated considerably in fruit. Calyx persistent, 5 lobed, divided to the middle [or base], usually accrescent, glabrous [or pubescent]. Corolla blue, rarely pink or white, funnelform, trumpet shaped [campanulate, or tubular]; limb shorter [or longer] than tube, spreading, shallowly undulate; throat open, with [or very rarely without] 5 inconspicuous (minute) [or conspicuous] faucal folds (fornices) alternating with stamens; tube long [to very short], densely pubescent within [or glabrous] at the base [or near the middle]. Stamens 5; filaments inserted below the corolla throat, longer [to shorter] than anthers; anthers exerted [or included]. Ovary deeply 5 lobed; style slender, longer [or shorter] than corolla tube; stigma entire. Nutlets 4 or fewer by abortion, rugose [or smooth and utricle-like], obtuse [or acute] at apex, wingless [or narrowly winged]; attachment scars ventral, slightly [or considerably] above nutlet base; gynobase short-conical, usually intruded between the nutlets. Base chromosome number 6. (*Pneumaria* Hill, 1764, nom. rejic. Including *Casselia* Dumort., *Cerinthodes* Ludwig, *Hippoglossum* C. J. Hartman ex Lilja, *Platynema* Schrader, *Oreocharis* Lindley, *Steenhammera* Reichenb., *Winkleria* Reichenb.) TYPE SPECIES: *M. pulmonarioides* Roth = *Pulmonaria virginica* L. = *M. virginica* (L.) Pers. ex Link. (Name honoring the German botanist Franz Karl Mertens, 3 April 1764–19 June 1831.) — BLUEBELL, LUNGWORT.

A well-defined genus of about 45 species, of which 24 are indigenous to North America, 15 to central Asia, Mongolia, and Siberia, and six to the Himalayas and Tibet (Popov). Only three species of *Mertensia* reach eastern North America (Fernald; Williams, 1937), and only *M. virginica* grows in the southeastern United States.

Mertensia virginica (*Pulmonaria virginica*, *M. pulmonarioides*; see Williams for nine additional synonyms), bluebell, Virginia bluebell, Roanoke bell, cowslip, Virginia cowslip, $2n = 24$, grows in rich woods, bottomlands, flood-plain woodlands, valley fields, and in clearings, on alluvial banks of streams, and occasionally on rocky slopes and bluffs. It is distributed from New York and Ontario to Minnesota, south to Kansas, and into the Southeastern States. Williams's (1937) account of *M. virginica* included only Alabama and Tennessee in the Southeast, but the species is known to grow in North Carolina (Hommersand; Pittillo & Brown), South Carolina (Fernald; Small, 1933), northwestern Georgia (Jones & Coile), and northern Arkansas (Smith, 1978, 1988). *Mertensia virginica* is readily distinguished from all the other borages of the southeastern United States in having large (2.5–3 cm long), blue, trumpet-shaped corollas densely hairy within at base, exerted styles and anthers, and glabrous, glaucous leaves and stems.

Johnston (1924a, 1924b) argued that on the basis of the suprabasal, oblique attachment scar of the nutlets and the undivided stigmas, *Mertensia* should be placed in the tribe Eritrichieae, rather than in either the Lithospermeae (Gürke) or Borageae [Boragineae] (Bentham). In contrast, Riedl (1968) placed the genus in subtribe Trigonotidinae

of the Trigonotideae Riedl. The boundaries, distinguishing characters, and relationships of the Trigonotideae are discussed under the family treatment.

Williams (1937) assigned the North American species of *Mertensia* to three sections. The monotypic sects. STEENHAMMERA (Reichenb.) A. Gray (nutlets smooth, utricle-like; leaves thick and fleshy) and NEURANTHIA L. O. Williams (nutlets rugose; corolla campanulate, not differentiated into limb and tube; roots cormlike) included *M. maritima* (L.) S. F. Gray and *M. bella* Piper, respectively. The remaining species were placed in sect. MERTENSIA (as *Eumertensia* A. Gray) (nutlets rugose; corollas divided into limb and tube). Popov studied the sectional classification of the genus on a worldwide basis and recognized six sections, including those treated by Williams (1937). However, he placed the generic type in the monotypic sect. TYFOMERTENSIA Popov instead of sect. MERTENSIA. The other sections recognized by Popov are MERTENSIA THE POPOV (monotypic; central Asia) and OREOCHARIS (Dcne.) Popov (six species; Himalayas, Tibet). In his sectional classification of *Mertensia*, Macbride (1916) placed great emphasis on the presence or absence of a ring of trichomes within the corolla, but subsequent authors (e.g., Popov; Williams, 1937) have ignored that feature.

Although *Mertensia* was previously associated with *Pulmonaria*, the two genera are not closely related. Johnston (1924b) suggested that *Mertensia* is closely related to *Anoplocaryum* Ledeb. (monotypic; eastern Siberia, Mongolia), from which it differs in the attachment of nutlets and in corolla shape. *Mertensia* is perhaps most closely related to *Trigonotis* Steven (50 species; Asia), from which it is easily distinguished by its medium-sized to large flowers, funnellform to tubular or campanulate corollas, and large, usually obscurely angled nutlets. In contrast, members of *Trigonotis* have small flowers, salverform corollas, and small, conspicuously tetrahedral nutlets.

Little is known about the reproductive biology of the various species of *Mertensia*. Meehan indicated that *M. virginica* is protandrous, and Pelton stated that *M. ciliata* (James) G. Don is protogynous. Geber showed that plants of the latter species are self-compatible and that the stigmas remain receptive for four to five days. Schneck observed more than a century ago that bumble bees extract the nectar of *M. virginica* by piercing holes or slits at the base of the corolla. Similar observations were made by Pelton with regard to the visitations of small bees of the genera *Colletes* and *Osmia* to the flowers of *M. ciliata*, and by Geber for bumble bees on this species. Knuth indicated that autogamy occurs in *M. maritima*, and Kerner von Marilaun reported heterostyly in *Mertensia* but gave no specific names.

As in many other members of the Boraginaceae, species of *Mertensia* show changes in flower color from pink at the bud stage to blue at anthesis. As indicated previously, such color change is probably related to the effects of fluctuations in pH on anthocyanin pigments.

Chromosome numbers have been reported for 16 species (ca. 35 percent of the total) of *Mertensia*, and apparently the genus is based



FIGURE 4. *Mertensia*. *M. virginica*: a, flowering plant, $\times 1/4$; b, enlarged portion of root, two stem bases (upper left) and rhizome (lower left), $\times 1/2$; c, inflorescence, $\times 1$; d, flower, $\times 2$; e, vertical section of flower—note small fornices between filaments at the throat of corolla, $\times 2$; f, flower after corolla has fallen to show gynoecium, $\times 5$; g, vertical section of same—note disklike gynobase below ovary lobes, $\times 5$; h, nutlets and accrescent calyx, $\times 3$; i, abaxial surface of nutlet—note attachment scar near the center of wing, $\times 6$; j, seed, oriented in same position as nutlet in “i”, $\times 6$; k, embryo, oriented as in seed, $\times 6$.

uniformly on $x = 6$ (Britton; Dawe & Murray, 1981b; Kovanda; Taylor & Taylor). The count $2n = 24$ has been reported for all species except the eastern Siberian *M. stylosa* (Fischer) DC., which has $2n = 48$. Accordingly, most species of the genus are tetraploid, but they are likely to be diploids based on 12. However, $2n = 12$ has not yet been reported in *Mertensia*. Dawe & Murray (1981b) found $2n = 72$ in *M. paniculata* (Aiton) G. Don, a species they considered to be a dodecaploid. Other authors have counted $2n = 24$ in that species.

Fertile hybrids between *Mertensia ciliata* and *M. alpina* (Torrey) G. Don have been noted by Cronquist (1984). He suggested (p. 212) that "frequent hybridization may be the basic cause of the taxonomic difficulties in the genus."

The chemistry of *Mertensia* has been poorly surveyed. The scant data on flavonoids in *M. viridis* A. Nelson (Bate-Smith) and *M. maritima* (Fedoreev *et al.*), fructose oligosaccharides in *M. virginica* (Pollard & Amuti), and pyrrolizidine alkaloids in *M. lanceolata* (Pursh) A. DC., *M. Bakeri* Greene, and *M. ciliata* (Li & Stermitz) do not show patterns of chemotaxonomic value. The last two species contain the alkaloids intermedine and/or lycopsamine.

Pollen of *Mertensia* is dumbbell shaped, tricolporate, and with the colpi equal in length (Ahn & Lee; Sahay). Clarke indicated that the pollen is 6- to 8-heterocolpate, and that the colpus margins are distally granular.

The peculiar root anatomy of *Mertensia maritima* has been described in detail by Skutch. Toward the end of the first year's growth, the stele of the root becomes divided into several individual strands, each consisting of one or few portions of the original ring of vascular bundles. The cambium in each of these strands then produces new xylem and phloem tissues, and these tissues are cut off from older tissues by the formation of periderm. The process is repeated annually, and the end result is the formation of a thick cable of numerous strands tied together by the abundant lateral roots. The lateral spreading of strands insures firm anchoring of *M. maritima* to coastal dunes, to which it is apparently restricted.

The nutlets of *Mertensia maritima* are utricle-like and are dispersed easily by sea water. The seeds remain viable after as many as 18 days of floating. They are also dispersed by wind (Scott). The rough surface of the nutlets of other species of *Mertensia* may help in their adherence to animal fur, and the light weight (ca. 0.0029 grams) of those of *M. ciliata* probably aids in their dispersal for short distances by wind (Pelton).

A few species of *Mertensia* are occasionally cultivated in rock gardens (Bailey *et al.*) and *M. virginica* is frequently grown in moist locations. Uphof stated that the Eskimos of Alaska consume the rhizomes of *M. maritima* for food, and Moerman indicated that *M. virginica* and *M. ciliata* are used as medicinal plants by the Cherokee and Cheyenne Indians, respectively.

REFERENCES:

- Under family references see AHN & LEE; BAILEY *et al.*; BAILLON; BATE-SMITH; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BRITTON; BRITTON & BROWN; BULL *et al.*; DE CANDOLLE; CHAPMAN; G. C. S. CLARKE; CORRELL & CORRELL (1972); CRONQUIST (1984); DEAN *et al.*; DUNCAN & FOOTE; FEDOREEV *et al.*; FERNALD; GATTINGER; GLEASON; GODFREY & WOOTEN; GOLDBLATT (1981); GREENE; GÜRKE; GUPTA; HOMMERSAND; HUNTER; JOHNSTON (1924a, b, 1932); JONES & COILE; KERNER VON MARILAUN; KNUTH; MOERMAN; MOHR; R. J. MOORE (1973,

1977); ORNDUFF (1968, 1969); POLLARD & AMUTI; POPOV (1953); RICKETT; RIDLEY; RIEDL (1968); SAHAY; SCHAEFER; SEIBERT; SHARP *et al.*; SMALL (1903, 1933); E. B. SMITH (1978, 1988); STEYERMARK; SYNGE; UPHOF; and VASUDEVAN.

BÖCHER, T. W. Biological distributional types in the flora of Greenland. Medd. Grøn. 106: 1-339. 2 pls. 1938. [*M. maritima*, 168.]

BRITTON, E. G. Wild plants needing protection. 14. "Virginia cowslip" or "bluebells" [*Mertensia virginica* (L.) DC.]. Jour. N.Y. Bot. Gard. 30: 209-211. pl. 304. 1929.

CURTIS, W. *Pulmonaria virginica*. Virginia lungwort. Bot. Mag. 5: pl. 160. [1 p. text.] 1791. [*M. virginica*.]

DALGAARD, V. Chromosome numbers in some vascular plants from the Disko Bugt area (West Greenland). Willdenowia 18: 243-252. 1988. [*M. maritima*, 245, fig. 1c, $n = 12$.]

DAWE, J. C., & D. F. MURRAY. In: Chromosome number reports LXX. Taxon 30: 68-80. 1981a. [*M. maritima*, 71, $2n = 24$.]

——— & ———. Chromosome numbers of selected Alaskan vascular plants. Canad. Jour. Bot. 59: 1373-1381. 1981b. [*M. Drummondii*, $2n = 24$; *M. paniculata*, $2n = 72$, 1378.]

FRANKS, J. W. *Mertensia*. In: T. G. TUTIN *et al.*, eds., Fl. Europaea 3: 109, 110. 1972. [*M. maritima*.]

GEBER, M. A. The relationship of plant size to self-pollination in *Mertensia ciliata*. Ecology 66: 762-772. 1985. [Hypothesis and mathematical models testing relationship of inbreeding rate to plant size; pollinators, breeding system.]

GERVAIS, C., & J. CAYOUILLE. Liste annotée de nombres chromosomiques de la flore vasculaire du nord-est de l'Amérique. IV. (English summary.) Nat. Canad. 112: 319-331. 1985. [*M. maritima*, 325, 326, $n = 12$, $2n = 24$.]

HARVEY, G. W. Seasonal alteration of photosynthetic unit sizes in three herb layer components of a deciduous forest community. Am. Jour. Bot. 67: 293-299. 1980. [*M. virginica*.]

HOOKE, J. D. *Mertensia alpina*. Bot. Mag. 101: pl. 6178. [2 pp. text.] 1875.

KHANNA, P. Ontogeny and embryology in *Mertensia*. Unpubl. Ph.D. dissertation, Univ. Oregon, Eugene. 1961.*

———. Embryology of *Mertensia*. Jour. Indian Bot. Soc. 43: 192-202. 1964. [*M. paniculata*, *M. platyphylla*; anatomy of anther, pericarp, and seed coat, micro- and megasporogenesis, embryogeny.]

KOVANDA, M. Chromosome numbers of miscellaneous United States dicotyledons. Rhodora 80: 431-440. 1978. [*M. virginica*, 434, $n = 12$.]

LEWIS, A. J. Distribution of *Mertensia maritima* (Boraginaceae) and subspecies of *Sagina nodosa* (Caryophyllaceae) on islands in Machias Bay, Maine. Rhodora 87: 431-435. 1985.

LI, Y., & F. B. STERNITZ. Pyrrolizidine alkaloids from *Mertensia* species of Colorado. Jour. Nat. Products 51: 1289, 1290. 1988. [*M. Bakeri*, *M. ciliata* (as *ciliolata*), *M. lanceolata*.]

LÖVE, Å., & D. LÖVE. In: IOPB chromosome number reports L. Taxon 24: 671-678. [*M. paniculata*, 674, $2n = 24$.]

LOVELL, H. B. The life story of three spring wild flowers. Wild Flower 19(4): 61-64; pls. 10, 11. 1942. [*Claytonia virginica*, *Mertensia virginica*, *Jeffersonia diphylla*.]

MACBRIDE, J. F. The true *Mertensias* of western North America. Contr. Gray Herb. 48: 1-20. 1916. [Thirty-two species; synonymy, distributions, keys, new taxa, sectional classification.]

MATTHEWS, V. B. An ecological life history of tall bluebell in Utah. 119 pp. M.S. thesis, Brigham Young Univ., Provo, Utah. 1965.*

- . A taxonomic study of *Mertensia* (bluebells) in Utah. *Proc. Utah Acad. Sci. Arts Lett.* **45**: 590–602. 1968. [Six species; descriptions, distributions, synonymies, key, maps.]
- MCDONOUGH, W. T. Carbohydrate reserves in *Mertensia arizonica* as related to growth, temperature, and clipping treatments. *Ecology* **50**: 429–432. 1969.
- MEEHAN, T. *Mertensia virginica*. Meehan's Monthly **4**: 33, 34. pl. 3. 1894. [Derivation of generic name; protandry noted.]
- MOORE, J. A. Morphology of the gynobase in *Mertensia*. *Am. Midl. Nat.* **17**: 749–752. 1936. [*M. brevistyla*, *M. humilis*, *M. maritima*, *M. virginica*; floral anatomy.]
- ORPET, E. O. The white mertensia. *Horticulture* **24**: 61. 1946. [Related notes by T. A. WESTON and M. R. JACOBS in *Ibid.* **5** and **25**, respectively.]
- PELTON, J. S. Variation patterns in four clones of *Mertensia ciliata*. *Madroño* **15**: 123–128. 1959. [Variation in length of calyx and corolla.]
- . An investigation of the ecology of *Mertensia ciliata* in Colorado. *Ecology* **42**: 38–52. 1961. [Distribution, habitats and associations, flowering, pollination, fruiting, dispersal, germination, vegetative reproduction, growth.]
- PITTILO, J. D., & A. E. BROWN. Additions to the vascular flora of the Carolinas. III. *Jour. Elisha Mitchell Sci. Soc.* **104**: 1–18. 1988. [*M. virginica* in Person County, North Carolina, 14.]
- POPOV, M. G. De generis *Mertensiae* Roth (Boraginaceae) systemate et evolutione comparatis speciebus americanis et asiaticis adnotationes. (In Russian.) *Bot. Mater. Notul. System.* **15**: 248–266. 1953. [Sectional classification, evolution within the genus, taxonomic notes, key, illustrations.]
- PRIER, P. V. Development of the helicoid and scorpioid cymes in *Myosotis lara* Lehm. and *Mertensia virginica* L. *Proc. Iowa Acad. Sci.* **67**: 76–81. 1960. [Scorpioid cymes of *Mertensia* develop from renewed meristematic activity at right angles to the previous flower primordium.]
- SCHENK, J. How bumblebees extract nectar from *Mertensia virginica* DC. *Bot. Gaz.* **12**: 111. 1887. [By making slits near the base of corolla tube.]
- SCOTT, G. A. M. Biological flora of the British Isles. *Mertensia maritima* (L.) S. F. Gray. *Jour. Ecol.* **51**: 733–742. 1963. [Distribution, morphology, habitats and communities, cytology, floral biology, dispersal.]
- SIMS, J. *Pulmonaria paniculata*. α . Blue-flowered panicle lungwort. *Bot. Mag.* **53**: pl. 2680. [2 pp. text.] 1826. [*M. paniculata*.]
- SKUTCH, A. F. Repeated fission of stem and root in *Mertensia maritima*—a study in ecological anatomy. *Ann. N.Y. Acad. Sci.* **32**: 1–52. pls. 1–9. 1930. [Habitats, seedling morphology and anatomy, stem and root anatomy, origin and importance of fission in the vascular tissue.]
- STARCHENKO, V. M. On the taxonomy of Far-Eastern species of the genus *Mertensia* Roth (Boraginaceae). (In Russian.) *Bot. Zhur.* **64**: 1666–1669. 1979. [*M. maritima*, *M. pterocarpa*, *M. pubescens*, *M. rivularis*; taxonomic notes, synonymy.]
- STEWART, N. F., & R. F. RANDALL. The past and present distribution of *Mertensia maritima* (L.) S. F. Gray in the British Isles. *B.S.B.I. News* **49**: 51. 1988.
- TAYLOR, R. L., & S. TAYLOR. Chromosome numbers of vascular plants of British Columbia. *Syesis* **10**: 125–138. 1977. [*M. oblongifolia*, 128, $2n = 24$.]
- WARD, D. E. Chromosome counts from New Mexico and southern Colorado. *Phytologia* **54**: 302–308. 1983. [*M. franciscana*, 304, $n = 12$.]
- WELCH, D. *Mertensia maritima* (L.) S. F. Gray on Scottish east coast. *B.S.B.I. News* **50**: 9. 1988.
- WILLIAMS, L. O. A monograph of the genus *Mertensia* in North America. *Ann. Missouri Bot. Gard.* **24**: 17–159. 1937. [Twenty-four species; morphology, distributions, descriptions, sections, key; the basic treatment.]
- . *Mertensia Drummondii* (Lehm.) G. Don. *Ibid.* **27**: 263, 264. pl. 30. 1940.

Tribe 2. ERITRICHIEAE (Bentham & J. D. Hooker) Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. 3A: 106. 1897.

7. **Plagiobothrys** Fischer & Meyer, Index Sem. Hort. Bot. Petrop. 2: 46. 1835.

Annual [or less frequently perennial], erect [or prostrate] herbs, usually small, often dichotomously branched, strigose [villous, or hispid], with appressed [or spreading], unbranched trichomes. Basal leaves not rosulate [or rosulate]; lower cauline leaves narrowly linear [or broad and variously shaped], opposite [or alternate]. Inflorescences ebracteate [or irregularly bracteate], densely flowered, helicoid cymes, elongating considerably in fruit and becoming racemelike [rarely remaining glomerulate]. Calyx 5 [to 8] lobed, persistent [or rarely circumscissile], usually densely pubescent, divided almost to the base [rarely to the middle] into lanceolate to linear [or oblong] lobes, sometimes accrescent in fruit. Corolla white [rarely pinkish]; limb rotately spreading, with imbricate, rounded lobes; throat with 5 intruded, yellow [or white] appendages (fornices); tube shorter than calyx. Stamens 5 [or 2-4], included, filaments very short. Ovary 4 lobed; ovules 4; style gynobasic, slender, usually short; stigma entire, capitate. Nutlets 4 (or fewer by abortion), erect, sessile [rarely stipitate], straight [or curved], ovate [lanceolate, or rarely cruciform], rugose [smooth, tuberculate, or ridged] on both surfaces, rounded [or keeled dorsally (abaxially)], usually strongly keeled ventrally (adaxially) above the attachment scar (areola); scars small, simple [or caruncle-like], subabasal [basal, or ventral (adaxial)], often placed at the end of the ventral (adaxial) keel [rarely extending along part of the keel]; gynobase short, pyramidal [or broad]. Base chromosome number 12. (Including *Allocarya* Greene, *Allocaryastrum* Brand, *Echidiocarya* A. Gray, *Echinoglochin* Brand, *Glyptocaryopsis* Brand, *Maccoya* F. Mueller, *Sonnea* Greene.) TYPE SPECIES: *P. rufescens* Fischer & Meyer (1835) = *Myosotis fulva* Hooker & Arnott (1830) = *P. fulvus* (Hooker & Arnott) I. M. Johnston. (Name derived from Greek *plagios*, oblique, and *bothrys*, a pit or excavation, in reference to the position of the attachment scar of the nutlet.)

A well-defined, taxonomically difficult genus of about 70 species. Munz's estimate of 100 species is somewhat exaggerated and Cronquist's (1984) of 50 species is below the mark. *Plagiobothrys* has two main centers of distribution and diversity: a Californian, where 39 species (18 endemic) grow, and a Chilean, where 19 (12 endemic) of the 25 South American species are found. Eight of the Californian species have ranges extending into Mexico, and four are disjunctly distributed between California and Chile. There are three indigenous species in Australia and one in eastern Asia. The genus is represented in the Southeastern States by a single naturalized species, the native range of which is primarily in the western United States and adjacent Canada.

Plagiobothrys hirtus (Greene) I. M. Johnston (*Allocarya hirta* Greene, *A. Scouleri* (Hooker & Arnott) Greene var. *hirta* (Greene) A. Nelson & Macbr., *P. Scouleri* var. *hirtus* (Greene) Johnston, *A. calycosa* Piper) was subdivided by Johnston (1935b) into three varieties, of which two (var. *hirtus* and var. *corallicarpus* (Piper) I. M. Johnston) are restricted to Oregon. The third, var. *figuratus* (Piper) I. M. Johnston (*Allocarya figurata* Piper, *Plagiobothrys figuratus* (Piper) I. M. Johnston ex Peck, *A. dichotoma* Brand), has spread from its native range in the Pacific Northwest eastward into the Southeast. Hommersand reported it from Durham and Orange counties, North Carolina, and Smith (1977, 1978) mapped it (as *P. hirsutus*) from Woodruff County, Arkansas. Chambers has argued that since vars. *hirtus* and *figuratus* are sympatric in several locations, do not hybridize, and are quite different in trichome morphology, they are best treated as distinct species. *Plagiobothrys figuratus* is a small annual with fibrous roots, opposite, linear lower leaves, usually paired cymes, white flowers with a yellow eye, and ovoid nutlets with rugose-tuberculate outer and inner surfaces and a small, lateral, suprabasal attachment scar. It grows in meadows, moist fields, and low grounds, as well as along roadbanks.

The generic limits of *Plagiobothrys* have been controversial, and Brand recognized as many as six minor segregates. Johnston (1923) presented a solid argument for the reduction of Greene's segregates to *Plagiobothrys*. He later (1932) defended vigorously his earlier position and showed that Brand's three segregate genera, which were based on poorly understood characters, should also be reduced to the synonymy of *Plagiobothrys*. The presence in *Allocarya* of opposite leaves, a feature overemphasized by Macbride and Piper as a basic generic character, was shown by Johnston (1923) to be unreliable because it is found to various degrees in *Plagiobothrys* and the related genus *Cryptantha* Lehm.

The sectional classification of *Plagiobothrys* needs some refinement, and the five sections recognized in Johnston's key (1923) require further study. Section ALLOCARYA (Greene) Johnston (lowermost leaves opposite; nutlets sessile, attached directly to the gynobase) is the largest in the genus and has representative species throughout the range of the genus.

Plagiobothrys is most closely related to *Amsinckia* Lehm. and *Cryptantha*. It is easily distinguished from *Amsinckia* in having undivided cotyledons and white flowers, with the corolla throat closed by five intruded appendages. *Amsinckia* has deeply bifid cotyledons and yellow flowers with a naked corolla throat. *Plagiobothrys* differs from *Cryptantha* in its nutlets with a small, lateral or nearly basal, caruncle-like attachment scar at the lower end of an adaxial (ventral) keel and in its flat or very low gynobase much shorter than the nutlets. In contrast *Cryptantha* has nutlets with an adaxial, narrowly open or closed, groove-like attachment scar along most of their length and has an elongated gynobase nearly equalling the nutlets.

Species limits within certain North American complexes of *Plagiobothrys* are problematic, and Johnston (1932, p. 5) stated that sect. *Allocarya* "presents bewildering individual variation, a wealth of transitional forms, and general lack of evident specific lines."

Chromosome numbers are known for about 11 species of *Plagiobothrys* (ca. 16 percent of total). Seven species are diploid ($2n = 24$) and four are polyploid with different base numbers. In *P. procumbens* (Colla) A. Gray (Argentina, Chile) triploid, tetraploid, and hexaploid counts have been reported (Grau 1971, 1988). Diploid populations of this species have not yet been found. Moore reported $n = 34$ for *P. calandrinoides* (Phil.) I. M. Johnston (Argentina, Chile), and Löve & Löve counted $2n = 54$ for the western North American *P. Scouleri*. Further counts are needed before the cytological evolution of the genus is resolved.

Although interspecific hybridization in *Plagiobothrys* was suspected by Greene more than a century ago, no evidence of its occurrence has been indicated by recent authors.

The reproductive biology of various species of *Plagiobothrys* has not been studied, and the genus has not been surveyed for secondary constituents. The occurrence of a red pigment in the roots of several species was reported by Norton, but the chemistry of this pigment has not been established. Pollen of several species is described as prolate to spheroidal, 3-zonocolporate (DiFulvio; Marticorena; Sahay).

Plagiobothrys does not have specialized means for dispersal. However, the disjunct distribution of individual species between California and Chile probably came about by long distance dispersal by migratory birds.

REFERENCES:

Under family references see BAILLON; DE CANDOLLE; CRONQUIST (1959, 1984); DiFulvio (1965b); FERNALD; HIGGINS (1979); HOMMERSAND; JOHNSTON (1924b, 1927, 1928, 1935b); NORTON; ORNDUFF (1968); RICKETT; SAHAY; SCHAEFER; E. B. SMITH (1978, 1988); and TOELKEN.

BRAND, A. *Plagiobothrys*. In: A. ENGLER, ed., *Das Pflanzenreich* IV. 252(Heft 97): 105–114. 1931. [Fourteen species; *Allocarya* (82 species; pp. 159–182), *Allocaryastrum* (five species; 99–101), *Echidiocarya* (monotypic; 158), *Echinoglochis* (eight species; 25–28), and *Glyptocaryopsis* (six species, 104, 105) also recognized, but all these were reduced by JOHNSTON (1932) to the synonymy of *Plagiobothrys*.]

CHAMBERS, K. L. The taxonomic relationships of *Allocarya corallicarpa* (Boraginaceae). *Madroño* 36: 280, 281. 1989. [*P. figuratus* subsp. *corallicarpa*, comb. nov.; suggested that *P. figuratus* and *P. hirtus* be recognized as distinct species.]

DiFulvio, T. E. Embriología de *Plagiobothrys tenellus* (Boraginaceae). (English summary.) *Kurtziana* 3: 183–199. 1966. [Floral anatomy, micro- and megasporogenesis, embryogeny.]

GRAU, J. Cytologische Untersuchungen an Boraginaceae II. (English summary.) *Mitt. Bot. Staatssamml. München* 9: 177–194. 1971. [Incl. *P. procumbens*, $2n = 72$; *P. tenellus*, $2n = 58 + 1B$.]

- . Chromosomenzahlen chilenischer Boraginaceae. *Ibid.* **27**: 29–32. 1988. [*P. collinus*, *P. fulvus*, *P. myosotoides*, *P. polycaulis*, and *P. pulchellus*, $2n = 24$; *P. procumbens* $2n = 36$, 48.]
- GREENE, E. L. Some West American Asperifoliae. *Pittonia* **1**: 8–23. 1887. [*Allocarya*, *Plagiobothrys*, *Sonnea*; generic limits, species and generic descriptions.]
- HIGGINS, L. C. A revision of the *Echidiocarya* section of *Plagiobothrys* (Boraginaceae). *Great Basin Nat.* **34**: 161–166. 1974. [Two species; descriptions, distributions, key.]
- JOHNSTON, I. M. A synopsis and redefinition of the genus *Plagiobothrys*. *Contr. Gray Herb.* **68**: 57–80. 1923. [Forty-nine species; synonymies, distributions, sectional classification, generic limits, key to species.]
- . The *Allocarya* section of *Plagiobothrys* in the western United States. *Contr. Arnold Arb.* **3**: 5–82. 1932. [Thirty-one species, key, descriptions, distributions; excellent and critical evaluation of Brand's segregates of *Plagiobothrys*; criticism of Piper's species concept and Macbride's arguments for the maintenance of *Allocarya*; see BRAND, MACBRIDE, and PIPER.]
- LÖVE, Á., & D. LÖVE. In: IOPB chromosome number reports LXVV. *Taxon* **31**: 342–368. [*P. Scouleri* (as subsp. *penicillatus*), 353, $2n = 54$.]
- MACBRIDE, J. F. Various spermatophytes. 5. A defense of *Allocarya*. *Publ. Field Mus. Bot.* **4**: 119–122. 1927. [Genus artificially delimited and characters separating it from *Plagiobothrys* not as reliable as author claimed; see JOHNSTON (1932).]
- MARTICORENA, C. Granos de polen de plantas chilenas I. *Gayana Bot.* **17**. 66 pp. 1968. [*Plagiobothrys*, 55–58; ten species surveyed.]
- MOORE, D. M. Chromosome numbers of Fuegian angiosperms. *Bol. Soc. Brot.* **II**. **53**: 995–1012. 1981. [*P. calandrinoides*, 1008, $n = 34$.]
- MUNZ, P. A. A California flora. *Frontisp.* + 1681 pp. Berkeley and Los Angeles. 1959. [*Plagiobothrys*, 577–587; 39 species recognized.]
- PIPER, C. V. A study of *Allocarya*. *Contr. U.S. Natl. Herb.* **22**: 79–113. 1920. [Seventy-nine species in 13 groups corresponding to sections; keys, descriptions, illustrations.]

8. *Amsinckia* Lehmann, *Sem. Hort. Bot. Hamburg* **1831**: 7. 1831, nom. cons.

Tap rooted, erect, usually bristly-hirsute to hispid, annual herbs. Leaves alternate, sessile, linear to lanceolate [or ovate], gradually reduced in size upward, usually obscurely veined, entire [rarely erose-dentate]. Inflorescences ebracteate, densely flowered helicoid cymes, considerably elongated and racemelike in fruit; flowers homostylous [or distylous]. Calyx divided to base into 5 [or by connation, 4 or 3] erect, persistent, lanceolate [or oblong] lobes, these equal [or unequal] in width, densely white [or rusty] bristly on the outside. Corolla tubular-salveriform [or funnellform], yellow [orange or reddish-orange], 1–2[–7] times as long as calyx, with 10 [or 20] nerves at the base; the throat open and glabrous [or closed by hairy crests]. Staminal filaments very short; anthers oblong, obtuse, included, inserted evenly [or irregularly] on the upper [or lower] half of the corolla tube. Style filiform, included; stigma capitate, somewhat emarginate. Nutlets 4, erect, angulate-ovoid, strongly keeled ventrally, keeled [or not] dorsally, unmarginated, verrucose [tessellate, or smooth]; areola inframedial and

located at lower end of adaxial (ventral) keel, small, carunculate, scar-like or groove shaped; gynobase frustate, about half as long as the nutlet. Cotyledons deeply 2 parted by a longitudinal slit. Base chromosome numbers 4-8, 13, 15, 17, 19. TYPE SPECIES: *Lithospermum lycopsoides* Lehm. = *A. lycopsoides* (Lehm.) Lehm. (Name honoring William Amsinck, burgomaster of Hamburg and early nineteenth-century patron of its botanical garden.)—FIDDLENECK, FIREWEED, TARWEED.

A well-defined but taxonomically difficult genus of about 15 species, all except one distributed primarily in the western United States, particularly California, the center of greatest diversity. The genus is represented in the southeastern United States by a single naturalized species.

Amsinckia Menziesii (Lehm.) A. Nelson & Macbr. (*Echium Menziesii* Lehm., *A. debilis* Brand, *A. Helleri* Brand, *A. idahoensis* M. E. Jones, *A. Kennedyi* Suksd., *A. micrantha* Suksd., *A. parviflora* Heller), $2n = 34$, grows in waste places and fields in Orange County, North Carolina, and was collected once (Ahles & Haesloop 22548, ncu) from waste ground around a wool-combing mill at Jamestown, Berkeley County, South Carolina.

Hommersand and Rickett reported *Amsinckia hispida* (Ruíz & Pavón) I. M. Johnston for the plant I am calling here *A. Menziesii*. As shown by Chater (1971), the former was based on *Lithospermum hispidum* Ruíz & Pavón (1799), a later homonym of *L. hispidum* Forsskål (1775). Therefore *A. hispida* should be known as *A. calycina* (Moris) Chater. *Amsinckia calycina*, a South American plant now naturalized in Africa and Europe, has become a serious weed of cereal crops in southern Australia. Small's (1933) report of *A. parviflora* from North Carolina, as well as Hommersand's and Rickett's of *A. hispida* from that state all represent misidentifications of the western North American *A. Menziesii*. Chater (1972) distinguished *A. Menziesii* from *A. calycina* on the basis of its setulose, instead of glabrous, nutlets and ebracteate, instead of basally bracteate, inflorescences. An examination of a large series of specimens shows that these alleged differences do not hold; perhaps it is one highly polymorphic species with two indigenous centers of distribution, North and South American. In that event, the species should be known under the older name, *A. Menziesii*.

Reports of *Amsinckia* from New England and adjacent eastern North America (Britton & Brown; Fernald) are based primarily on older introductions from the Pacific Northwest, and it is highly doubtful that the previously reported *A. intermedia* Fischer & Meyer, *A. lycopsoides*, and *A. Menziesii* are now present in New England. Pittillo & Brown reported *A. lycopsoides* from Jackson County, North Carolina, and listed *A. hispida* as a synonym. I have not seen their collection.

Amsinckia Menziesii and the bulk of the genus belong to sect. MURICATA Suksd., which is characterized by muricate to verrucose nutlets

and five distinct calyx lobes. It contains several highly variable species with poorly defined boundaries.

Species delimitation in *Amsinckia* is indeed difficult, and all except a few of the approximately 200 "new" species described by Suksdorf do not merit recognition. Most of the taxonomic difficulties encountered have resulted from the overemphasis by earlier workers on characters (e.g., nutlet size, shape, color; leaf shape; pubescence), the value of which in delimiting taxa is now considered to be insignificant. The account of Ray & Chisaki (1957a) is perhaps the most practical to date. Brand placed the 41 species he recognized in three sections, of which two are monotypic. It is doubtful, however, that his sectional classification is of practical value.

Amsinckia is easily distinguished from other members of the tribe Eritrichieae and from the remainder of the Boraginaceae in the South-eastern States in having a regular calyx; a yellow to orange, unappendaged corolla; an undivided stigma; four erect, trigonous nutlets that are attached near the middle; and bifid cotyledons.

The reproductive biology of *Amsinckia* has been studied fairly extensively. All except five species are homostylous, self-compatible, widely distributed weeds. Distyly occurs in the Californian endemic *A. Douglasiana* A. DC. ($2n = 12$), *A. furcata* Suksd. ($2n = 14$), *A. grandiflora* Kleeb. ex A. Gray ($2n = 12$), *A. lunaris* Macbr. ($2n = 8$), and *A. spectabilis* Fischer & Meyer ($2n = 10$). The first three species produce dimorphic pollen that is larger in the thrum (short-styled) than in the pin (long-styled) flowers. Furthermore, the thrum flowers are generally larger than the pin ones (Ganders, 1975a; Ray & Chisaki, 1957a). In *A. lunaris* heterostyly is peculiar in that the anthers are inserted at two levels on the corolla tube, and style length occurs in different combinations in relation to the position of anthers (Ray & Chisaki, 1957a, b). Heterostylous and homostylous forms are found within and among populations of *A. furcata*, *A. lunaris*, and *A. spectabilis*.

As in most other distylous plants, the genetic basis of the difference in style length in *Amsinckia* is controlled by a single gene: pin plants are homozygous recessive and thrum plants are heterozygous. Ganders (1975a) and Ray & Chisaki (1957a) indicated that all five heterostylous species of *Amsinckia* are self-compatible. However, several authors (e.g., Casper *et al.*; Ornduff; and Weller & Ornduff, 1977, 1989) have demonstrated that at least *A. Douglasiana* and *A. grandiflora* have cryptic self-incompatibility. It has been found that crosses between morphs produce more seeds than self-pollination does, and that selfing produces more seeds than illegitimate intramorph pollination. Casper and colleagues suggested that the apparent cryptic self-incompatibility in *A. Douglasiana* is caused by ovule abortion, but Weller & Ornduff (1989) have clearly demonstrated that its cause in *A. grandiflora* can be attributed to differential pollen tube growth, which is markedly higher following intermorph than after intramorph crosses. Although the heterostylous plants produce many seeds, Ornduff noted that the

homostylous, self-compatible taxa are more aggressive and are gradually displacing *A. grandiflora*.

Chromosome numbers have been reported for all except one species of *Amsinckia* (Ray & Chisaki, 1957b, c). The single species, *A. carinata* Nelson & Macbr., is known only from the type collection that was made in 1896 and has not been rediscovered since (Ray & Chisaki, 1957a). Aneuploidy is well documented in *A. intermedia* ($2n = 30, 34, 38$) and *A. Menziesii* ($2n = 16, 26, 34$). The remaining species have constant numbers. The lowest number, $2n = 8$, has been reported for *A. lunaris*. Ray & Chisaki (1957b, c) observed that the heterostylous species have haploid chromosome numbers of four to seven, whereas the homostylous taxa have numbers of seven, eight, twelve, and higher. They considered the large-flowered, heterostylous taxa to be primitive and the small-flowered, homostylous taxa to be derived. Evolution among the heterostylous species was believed to have involved a gradual decrease in chromosome number from $n = 7$ to $n = 4$. Evolution to homostyly apparently has occurred more than once in the genus.

Natural interspecific hybridization apparently has occurred between *Amsinckia intermedia* and each of *A. lycopsoides* and *A. Menziesii*. The putative hybrids are partially fertile. All three species belong to sect. MURICATA, the other members of which are also potentially capable of hybridization, but species of this section do not hybridize with those of other sections (Ray & Chisaki, 1957c).

Four species of *Amsinckia* have been surveyed for pyrrolizidine alkaloids (Culvenor & Smith, Roitman). All four have high concentrations of intermedine and lycopsamine. In *A. intermedia* the alkaloids sin-camidine and echiumine were also found, and small concentrations of the last were detected in *A. calycina* (as *A. hispida* and *A. lycopsoides*). The increasing interest in the alkaloidal contents of the weedy species of *Amsinckia* is attributed to the poisonous effects of these compounds on livestock that feed on hay contaminated with these borages. Bees foraging on plants containing pyrrolizidine alkaloids transfer the poisonous compounds to their honey.

Esau & Magyarosy (1979a) observed unusual crystalloids in the nuclei of developing sieve-tube elements of *Amsinckia Douglasiana*. The crystalloid consists of two radiating components that form three to seven alternating blocks extending through its entire length. One of the components consists of four-sided, closely packed tubules, whereas the other has six-sided, wider, loosely arranged tubules that form a paracrystalline aggregate. These proteinaceous crystalloids become fragmented or disaggregated as the nucleus of the maturing sieve tube element disappears.

Except for their poisonous effects on livestock and for being noxious weeds that cause skin irritation, *Amsinckia* has no economic importance.

REFERENCES:

- Under family references see AHN & LEE; BAILLON; BENTHAM; BOLKHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; G. C. S. CLARKE; CORRELL & JOHNSTON; CRONQUIST (1959, 1984); DiFULVIO (1965b); EVERIST; GANDERS; GLEASON; GOLDBLATT (1985); JODIN; JOHNSTON (1924a, 1927, 1935b); JOHNSTON *et al.*; KAUL; KINGSBURY; LEWIS & ELVIN-LEWIS; LUBBOCK; MARTICORENA; MOERMAN; R. J. MOORE; MUENSCHER; RICKETT; SAHAY; SMALL (1933); SMITH & CULVENOR; STREY; THORSCH & ESAU; TOELKEN; VUILLEUMIER; and WILLAMAN & LI.
- ANONYMOUS. Endangered and threatened wildlife and plants: proposal of endangered status and critical habitat for the large flowered fiddleneck (*Amsinckia grandiflora*.) Fed. Regist. USA 49: 19534-19538. 1984.*
- BRAND, A. *Amsinckia*. In: A. ENGLER, ed., Das Pflanzenreich IV. 252(Heft 97): 204-216. 1931. [Forty-one species in three sections.]
- CASPER, B. B., L. S. SAYIGH, & S. S. LEE. Demonstration of cryptic incompatibility in distylous *Amsinckia Douglasiana*. Evolution 42: 248-253. 1988. [Comparison of seed set following legitimate and illegitimate pollinations; determination of competitive ability of pollen by using genetic markers unlinked to gene controlling style length.]
- CHATER, A. O. *Amsinckia* Lehm. In: V. H. HEYWOOD, ed., Flora Europaea. Notulae systematicae ad floram Europaeam spectantes. 11. Bot. Jour. Linn. Soc. 64: 353-381. 1971. [*A. calycina* replaces *A. hispida*, 380.]
- . *Amsinckia*. In: T. G. TUTIN *et al.*, eds., Fl. Europaea 3: 110. 1972. [*A. Douglasiana*, *A. calycina*, *A. intermedia*, *A. lycopsoides*, *A. Menziesii*.]
- . *Amsinckia* in Britain. B.S.B.I. News 9: 12-14. 1975. [Five species; notes and key.]
- CONNOR, D. J. Seed production and seed germination in *Amsinckia hispida*. Austral. Jour. Exper. Agr. Animal Husb. 5: 495-499. 1965.*
- CULVENOR, C. C. J., & L. W. SMITH. The alkaloids of *Amsinckia* species: *A. intermedia* Fisch. & Mey., *A. hispida* (Ruiz & Pav.) Johnst. and *A. lycopsoides* Lehm. Austral. Jour. Chem. 19: 1955-1964. 1966.
- ESAU, K., & A. C. MAGYAROSY. A crystalline inclusion in sieve element nuclei of *Amsinckia*. I. The inclusion in differentiating cells. Jour. Cell Sci. 38: 1-10. 1979a; II. The inclusion in maturing cells. *Ibid.* 11-22. 1979b.
- & ———. Nuclear abnormalities and cytoplasmic inclusions in *Amsinckia* infected with the curly top virus. Jour. Ultrastruct. Res. 66: 11-21. 1979c. [*A. Douglasiana*; viral particles identified.]
- FAEGRI, K. Om de i Norden iaktatte *Amsinckia*-arter. En systematisk orientering. Bergens Mus. Årbok 8: 1-35. 1929. [Twenty-three species; key, notes, illustrations.]
- FRIEND, D. A. Chromosome number in a Victorian population of *Amsinckia calycina*. Austral. Weeds 1: 7, 8. 1982. [$n = 17$, $2n = 34$.]
- GANDERS, F. R. Heterostyly, homostyly and fecundity in *Amsinckia spectabilis* (Boraginaceae). Madroño 23: 56-62. 1975a. [Distribution and seed set of various flower morphs.]
- . Mating patterns in self-incompatible distylous populations of *Amsinckia* (Boraginaceae). Canad. Jour. Bot. 53: 773-779. 1975b. [*A. furcata*, *A. spectabilis*.]
- . Pollen flow in distylous populations of *Amsinckia* (Boraginaceae). *Ibid.* 54: 2530-2535. 1976. [*A. Douglasiana*, *A. furcata*; stigmas of pin flowers capture more pollen than those of thrum flowers, disassortative pollination in thrum flowers.]

- . The effect of breeding system on genetic diversity in *Amsinckia spectabilis* (Boraginaceae). Pp. 17–24 in 2nd Internatl. Congr. Syst. Evol. Biol., Vancouver, Canada. 1980.*
- , S. K. DENNY, & D. TSAI. Breeding systems and genetic variation in *Amsinckia spectabilis* (Boraginaceae). *Canad. Jour. Bot.* **63**: 533–538. 1985. [Allelic variation at 17 loci using starch-gel electrophoresis; heterostylous plants have highest genetic variability.]
- JOHNSON, A. E., R. J. MOLYNEUX, & G. B. MERRILL. Chemistry of toxic range plants. Variation in pyrrolizidine alkaloid content of *Senecio*, *Amsinckia*, and *Crotalaria* species. *Jour. Agr. Food Chem.* **33**: 50–55. 1985.*
- KAMB, P. Chromosome numbers in the genus *Amsinckia*. *Madroño* **11**: 305–307. 1952. [Haploid counts for eight species.]
- KHARKEVICH, S. S. *Amsinckia* Lehm. (family Boraginaceae)—a new genus for the flora of the U.S.S.R. (In Russian.) *Bot. Zhur.* **60**: 696–698. 1975. [*A. Menziesii*; fig.]
- LASSEN, P. Om gullört, *Amsinckia* in Norden. (English summary.) *Sv. Bot. Tidskr.* **82**: 141–150. 1988. [Seven species; history of introductions, current status, distributions in Scandinavia, illustrations, key.]
- LOON, J. C. VAN. In: IOPB chromosome number reports. LXXVII. *Taxon* **31**: 761–777. 1982. [*A. intermedia*, 763, $2n = 34$.]
- MACBRIDE, J. F. A revision of the North American species of *Amsinckia*. *Contr. Gray Herb.* **49**: 1–16. 1917. [Twenty-three species; keys, synonymy, distributions, notes.]
- MUNZ, P. A. A California flora. *Frontisp.* + 1681 pp. Berkeley and Los Angeles. 1959. [*Amsinckia*, 587–589; nine species recognized.]
- ORNDUFF, R. The reproductive system of *Amsinckia grandiflora*, a distylous species. *Syst. Bot.* **1**: 57–66. 1976. [Distribution, pollinators, seed production, cryptic self-incompatibility.]
- PANTONE, D. J. Host range of *Anguina amsinckiae* within the genus *Amsinckia*. *Rev. Nematol.* **10**: 117–119. 1987.*
- PITTILO, J. D., & A. E. BROWN. Additions to the vascular flora of the Carolinas. III. *Jour. Elisha Mitchell Sci. Soc.* **104**: 1–18. 1988. [*Amsinckia lycopsoides* from Jackson County, North Carolina, 14.]
- POPOVA, T. N., Z. A. GUDZHINSKAS, & E. A. ZEMSKOVA. The genus *Amsinckia* (Boraginaceae) in the flora of the U.S.S.R. (In Russian.) *Bot. Zhur.* **75**: 276–278. 1990.
- RAY, P. M., & H. F. CHISAKI. Studies on *Amsinckia*. I. A synopsis of the genus, with a study of heterostyly in it. *Am. Jour. Bot.* **44**: 529–536. 1957a. [Fourteen species; key, synonymy, distributions; occurrence and genetics of heterostyly]; II. Relationships among the primitive species. *Ibid.* 537–544. 1957b. [Chromosome numbers, heterostyly and homostyly, evolutionary trends.]; III. Aneuploid diversification in the Muricatae. *Ibid.* 545–554. 1957c. [Chromosome numbers, natural and artificial interspecific hybridization.]
- ROITMAN, J. N. The pyrrolizidine alkaloids of *Amsinckia Menziesii*. *Austral. Jour. Chem.* **36**: 769–778. 1983. [Five alkaloids identified.]
- SCHOENTAL, R., M. E. FOWLER, & A. COADY. Islet cell tumors of the pancreas found in rats given pyrrolizidine alkaloids from *Amsinckia intermedia* Fisch. & Mey. and from *Heliotropium supinum* L. *Cancer Res.* **30**: 2127–2131. 1970.
- SUKSDORF, W. Untersuchungen in der Gattung *Amsinckia*. *Werenda* **1**: 47–113. 1931. [Treatment of 236 species, of which about 200 were described as new by the author!]
- WELLER, S. G., & R. ORNDUFF. Cryptic self-incompatibility in *Amsinckia grandiflora*. *Evolution* **31**: 47–51. 1977. [Mixed pollinations of the two morphs produced equal numbers of pin and thrum plants; fewer pollen tubes reach the base of style following intramorph than in intermorph crosses.]

——— & ———. Incompatibility in *Amsinckia grandiflora* (Boraginaceae): distribution of callose plugs and pollen tubes following inter- and intramorph crosses. *Am. Jour. Bot.* **76**: 277–282. 1989. [Differential distribution of pollen-tube growth believed to be the cause of cryptic self-incompatibility.]

WELSH, N. S. *Amsinckia*, a noxious weed of increasing importance. *Jour. Agr. Victoria* **63**: 383–386. 1965.*

9. *Hackelia* Opiz in Berchtold, *Oekon.-techn. Fl. Böhmens* **2**(2): 147. 1839.

Coarse, erect [or ascending], biennial [perennial, or very rarely annual] herbs, antrorsely or retrorsely strigose or hirsute throughout. Basal leaves petiolate, entire, withering before anthesis [or persistent and forming well-developed rosettes]; cauline leaves alternate, narrowed to a petiole-like base [or sessile and somewhat clasping], secondary veins conspicuous [or inconspicuous]. Inflorescences paniculate helioid cymes, bracteate at base [or ebracteate throughout]; flowers small or showy; fruiting pedicels deflexed or recurved. Calyx 5 lobed, divided nearly to base, slightly accrescent in fruit, the lobes spreading to deflexed. Corolla pale blue, white [pink, yellow, or greenish marked with blue], usually with a yellow center, somewhat rotate [rarely subcampanulate]; throat with well-developed, trapeziform, intruded appendages alternating with and above the stamens; lobes imbricate, rounded; tube shorter [equalling or sometimes longer] than the calyx lobes, usually with a crest near the base. Stamens 5, included [or rarely exerted], all inserted at same level near middle of corolla tube; anthers oblong or elliptic. Ovary deeply 4 lobed, ovules 4; stigma capitate. Nutlets 4 (or fewer by abortion), ovate [to lanceolate], erect, ventrally (adaxially) keeled, attached to the gynobase with a broad, medial or submedial areola, the margin with subulate, glochidiate prickles that are distinct [or confluent] at base, the dorsal (abaxial) surface with [or without] intramarginal glochidiate prickles; gynobase pyramidal, much shorter than the nutlets; style sharply differentiated from the gynobase, usually hidden between the nutlets. Base chromosome number 12. TYPE SPECIES: *Myosotis deflexa* Wahl. = *H. deflexa* (Wahl.) Opiz. (Name honoring Joseph Hackel, 5 March 1783–25 Nov. 1869, a Czech botanist.)

A genus of about 45 species primarily of the western United States where 29 species grow. There are about six species in Mexico, two of which also occur in the United States, and one, *Hackelia mexicana* (Schlect. & Cham.) I. M. Johnston, that is widespread in Central America and occurs south into Ecuador and Peru. *Hackelia revoluta* (Ruíz & Pavón) I. M. Johnston is endemic to South America. There are six species indigenous to eastern Asia, in addition to *H. deflexa*, which is widespread in both Europe and North America. The genus is represented in the southeastern United States by a single species.

Hackelia virginiana (L.) I. M. Johnston (*Myosotis virginiana* L., *Echinosperrum virginianum* (L.) BSP., *Rochelia virginiana* (L.) Roemer & Schultes, *Lappula virginiana* (L.) Greene, *E. virginicum*

(L.) Lehm., *Cynoglossospermum virginicum* (L.) Kuntze, *Cynoglossum Morisonii* DC.), stickseed, beggar's lice, $2n = 24$, grows exclusively east of the 98th meridian and is distributed from southeastern North Dakota east through Ontario and Quebec into New England (excluding Maine), south into all the Southeastern States (except Florida and also absent from the Coastal Plain), and west into northeastern Texas. Hommersand indicated that the species grows in Florida, but neither Gentry & Carr nor Ward & Fantz have recorded it from there. It is readily distinguished from other southeastern Boraginaceae by its biennial habit; height (to 1.5 m); small, white to pale blue corollas; appendaged corolla throat; recurved fruiting pedicels; and glochidiate nutlets attached laterally to a pyramidal gynobase.

Hackelia has been previously reduced to the synonymy of *Lappula*, but almost all recent floristic treatments recognize both as independent genera. Chater's account of *Lappula* for *Flora Europaea*, in which he united these genera under the latter, is, however, an exception. Authors uniting *Hackelia* and *Lappula* are often impressed by the occurrence in both of glochidiate prickles on the nutlets. As indicated by Johnston (1923), these structures are not dependable in assessing immediate relationships, and characters of the gynobase are far more important in the delimitation of genera. *Hackelia* is easily distinguished on the basis of its usually perennial or biennial (very rarely annual) habit; inflorescences ebracteate throughout or bracteate in the lowermost portion only; recurved or deflexed fruiting pedicels; deflexed or spreading calyx lobes; styles sharply differentiated from the gynobase and often surpassed by the nutlets; nutlets with broad, medial, ventral (adaxial) attachment areolae; and a pyramidal gynobase shorter than the nutlets. In contrast, species of *Lappula* are annuals with the inflorescences bracteate throughout, fruiting pedicels erect, calyx lobes ascending or erect, styles not differentiated from the gynobase apex and usually exserted above the nutlets, nutlets attached along a narrow ventral (adaxial) keel, and subulate gynobases nearly equalling the nutlets. In fact, Johnston (1923, 1927) and Gentry & Carr associated *Hackelia* only loosely with *Lappula* and suggested that the former is very closely related to *Eritrichium* Schrader (25 species of Asia) and to *Selkirkia* Hemsley (monotypic; Juan Fernández Islands, Chile). The resemblance of *Hackelia* to *Eritrichium* is so great that Johnston (1923, p. 43) suggested that "with much justification the two genera might be merged." He indicated that *Hackelia* has broad, thin leaves; stems 2–10 dm tall; reflexed or spreading calyx lobes; and glochidiate prickles on the nutlets, whereas *Eritrichium* has small, firm leaves; stems usually to 2 dm tall; erect calyx lobes; and nonglochidiate prickles. However, the reduction of *Hackelia* to a subgenus of *Eritrichium* (Wang *et al.*) requires careful re-evaluation.

Brand divided *Hackelia* into sect. *HACKELIA* (as *Euhackelia* Brand) (fruiting pedicels reflexed), which included 37 species of almost exclusively North American distribution, and sect. *ERITRICHIASTRUM* Brand (fruiting pedicels erect) that comprised four eastern Asiatic species.

He adopted a narrow species concept, and, as pointed out by Gentry & Carr, three species of the latter section are now retained in *Eritrichium*.

Chromosome numbers have been recorded for 21 species of *Hackelia* (ca. 51 percent of the total). The majority of species are apparently based uniformly on 12. According to Gentry & Carr, however, Sabold reported $n = 8$ for *H. mundula* (Jepson) Ferris and *H. velutina* (Piper) I. M. Johnston, $n = 10$ for *H. nervosa* (Kellogg) I. M. Johnston, and $n = 11$ for *H. micrantha* (Eastw.) J. L. Gentry. Tetraploidy has played an important role in the evolution of the genus and has been recorded for at least 11 species. *Hackelia deflexa* is known as diploid ($2n = 24$) in several parts of the world, but Vasudevan reported it (as *Lappula*) to be a tetraploid ($2n = 48$).

The pollen of *Hackelia* has been studied in several species; it is apparently uniform in the genus. It is dumbbell shaped, tricolporate and has three alternating pseudocolpi and a smooth surface (Ahn & Lee; Gentry & Carr; Palacios-Chávez & Quiroz-García; Sahay).

Putative intergeneric hybridization between *Hackelia* and *Lappula* was suggested by Cronquist, who indicated that *H. cinerea* (Piper) I. M. Johnston and *L. Redowskii* (Hornem.) Greene hybridize near Rig-gins, Idaho. However, Gentry & Carr studied the plants of that area and stated that they represent a variable population of *H. cinerea*. Although in the northern portions of its range *Hackelia virginica* is sympatric with *H. deflexa* var. *americana* (A. Gray) Fern. & I. M. Johnston, no intermediates have been found (Gentry & Carr). Morphological evidence supporting hybridization of *H. diffusa* (Douglas ex Lehm.) I. M. Johnston var. *arida* (Piper) R. L. Carr and *H. venusta* (Piper) St. John has been presented by Gentry & Carr. One specimen (*Maguire 18871*, GH) was annotated by Gentry as a putative hybrid of *H. floribunda* (Lehm.) I. M. Johnston and *H. patens* (Nutt.) I. M. Johnston var. *patens*.

The phytochemistry of *Hackelia* is poorly surveyed. Hagglund *et al.* found in *H. floribunda* the pyrrolizidine alkaloids latifoline-N-oxide and latifoline in a ratio of 10:1. The fatty acids of *H. deflexa* were analyzed by Tétényi, who found high concentrations (43 percent) of oleic acid, moderate amounts (ca. 29 percent) of linoleic acid, and low levels (14 percent) of two isomers of linoleic acid.

Most of the American species of *Hackelia* are either narrow endemics or restricted to specific edaphic conditions, and only a few (e.g., *H. deflexa* var. *americana*, *H. micrantha*, and *H. virginiana*) have broad geographic ranges. The presence of glochidiate prickles on the nutlets is evidently an adaptation to dispersal by adhesion to passing animals, including humans. The intermingling of prickles of adjacent nutlets usually causes the four nutlets of a fruit to be detached and dispersed as a unit. The entire infructescence or portions of it are occasionally dispersed (Gentry & Carr).

The genus has little or no economic importance. Moerman and Taylor indicated that the Cherokee Indians prepare from the roots of *Hackelia virginiana* a decoction to relieve itching and kidney troubles and

an ointment, prepared with bear oil, to treat tumors. The species is a noxious weed in portions of its range.

REFERENCES:

- Under family references see AHN & LEE; CORRELL & CORRELL; CRONQUIST (1959); DUNCAN & KARTESZ; FERNALD; GIBSON; GLEASON; GOLDBLATT (1981, 1984, 1985); GUNN *et al.*; HIGGINS (1979); HILGER (1985); HOMMERSAND; JOHNSTON (1924b, 1927, 1948); JONES & COILE; MACROBERTS; J. S. MILLER (1988); MOERMAN; R. J. MOORE (1973, 1977); MUENSCHER; NOWICKE; POPOV (1953); RICKETT; SAHAY; SCHAEFER, SHARP *et al.*; E. B. SMITH (1978, 1988); STEYERMARK; TAYLOR; TÉTÉNYI; and VASUDEVAN.
- BRAND, A. In: A. ENGLER, ed., Das Pflanzenreich IV. **252**(Heft 97): 117–135. 1931. [Forty-one species in two sections.]
- CARR, R. L. A new species of *Hackelia* (Boraginaceae) from Oregon. *Madroño* **22**: 390–392. 1974. [*H. ophiobia*, sp. nov.; relationships, illustrations.]
- GENTRY, J. L., JR. A new combination and a new name in *Hackelia* (Boraginaceae). *Madroño* **21**: 490. 1972. [The new name *H. Cronquistii* and the new combination *H. micrantha* proposed.]
- . Studies in the genus *Hackelia* (Boraginaceae) in the western United States and Mexico. *Southwest. Nat.* **19**: 139–146. 1974. [Six species; distributions, taxonomic notes, new combinations, and new varieties.]
- . Current status of the genus *Hackelia* (Boraginaceae) in Wisconsin. *Michigan Bot.* **17**: 48. 1978. [Genus represented in Wisconsin by *H. deflexa* var. *americana*.]
- . *Hackelia*. In: D. L. NASH & N. P. MORENO, Boraginaceae. Fl. Veracruz **18**: 63–69. 1981. [*H. mexicana*, *H. stricta*.]
- & R. L. CARR. A revision of the genus *Hackelia* (Boraginaceae) in North America, north of Mexico. *Mem. N. Y. Bot. Gard.* **26**: 121–227. 1976. [Twenty-eight species; morphology, cytology, pollen, dispersal, distribution, descriptions, generic relationships, key, maps, illustrations; the basic treatment.]
- HAGGLUND, K. M., K. M. L'EMPEREUR, M. R. ROBY, & F. R. STERMITZ. Latifoline and latifoline-N-oxide from *Hackelia floribunda*, the western false forget-me-not. *Jour. Nat. Prod.* **48**: 638, 639. 1985. [Isolation and identification of these two pyrrolizidine alkaloids.]
- JOHNSTON, I. M. Restoration of the genus *Hackelia*. *Contr. Gray Herb.* **68**: 43–48. 1923. [Differences between *Hackelia* and *Lappula*; 26 new combinations, notes, synonymy.]
- L'EMPEREUR, K. M., Y. LI, F. R. STERMITZ, & L. CRABTREE. Pyrrolizidine alkaloids from *Hackelia californica* and *Gnaphaela latipennis*, an *H. californica*-hosted arctiid moth. *Jour. Nat. Products* **52**: 360–366. 1989. [Two new analogues of latifoline isolated and characterized from *H. californica*.]
- LÖVE, Á, & D. LÖVE. In: IOPB chromosome number reports. LXXV. *Taxon* **31**: 342–368. 1982. [*H. deflexa* subsp. *americana*, 353, 2n = 24.]
- PALACIOS-CHÁVEZ, R., & D. L. QUIROZ-GARCÍA. Catálogo palinológico para la flora de Veracruz. No. 26. Family Boraginaceae. Género *Hackelia*. (English summary.) *Biotica Méx.* **10**: 289–292. 1985. [*H. mexicana*, pollen heterocolpate-tricolpate, three true colpae alternating with three longer pseudocolpae.]
- PINKAVA, D. J., R. K. BROWN, J. H. LINDSAY, & L. A. MCGILL. In: IOPB chromosome number reports. LXIV. *Taxon* **23**: 373–380. 1974. [*H. floribunda*, 379, 2n = 24.]
- PIPER, C. V. Notes on the biennial and perennial West American species of *Lappula*. *Bull. Torrey Bot. Club* **29**: 535–549. 1902. [Nineteen species, reduced by JOHNSTON (1923) to 12 species of *Hackelia*.]

- PULLEN, T. M., S. B. JONES, JR., & J. R. WATSON, JR. Additions to the flora of Mississippi. *Castanea* 33: 326-334. 1968. [*H. virginica* from Issaquena and Bolivar counties, 332.]
- SABOLD, D. I. A cytotaxonomic and ecological study of the species of *Hackelia* occurring in the central Sierra Nevada. Unpubl. M.S. thesis, San Jose State College, California. 1966.*
- SHARP, A. J., & A. BAKER. First and interesting reports of flowering plants in Tennessee. *Castanea* 29: 178-185. 1964. [*H. virginica* occurs in scattered localities, except for western Tennessee, 183.]
- SHULTZ, L. M., & J. S. SHULTZ. A new species of *Hackelia* (Boraginaceae) from Utah. *Brittonia* 33: 159-161. 1981. [*H. ibapensis*, sp. nov.; relationships, illustration, key distinguishing the species from *H. Sharsmithii*.]
- SPELLENBERG, R. Documented chromosome numbers of plants. *Madroño* 19: 134-136. 1967. [*H. cinerea*, 136, $2n = 48$.]
- WANG, W.-T., Y.-S. LIAN, & J.-Q. WANG. A study of the genus *Eritrichium* from China. (In Chinese.) *Bull. Bot. Lab. North-East Forest Inst.* 9: 31-52. 1980. [*Hackelia* reduced to a subgenus of *Eritrichium* and included in two sections, three series, and 31 species; new taxa.]

10. *Lappula* Moench, Method. 416. 1794.

Small annual or rarely biennial herbs with fine, simple, spreading to appressed trichomes that are rarely tuberculate at base. Stems simple or much branched at base, erect [or decumbent]. Basal and lowermost cauline leaves sessile or subsessile, tapering at base, entire. Cymes bracteate throughout, elongating considerably and becoming raceme-like; flowers actinomorphic; pedicels erect, short [or rarely obsolete]. Calyx minute at anthesis, deeply divided almost to the base into 5 linear or lanceolate lobes, these spreading [or erect] in fruit, persistent [or caducous]. Corolla small, blue [rarely white], funnellform with a short tube [or rotate]; lobes rounded, imbricate; throat closed by 5 gibbous, intruded appendages. Filaments very short, the subsessile anthers inserted near middle of the tube. Ovary 4 lobed, 4 ovulate; style included; stigma entire, capitate. Nutlets 4, erect, ovoid [pyriform or triangular], glochidiate, tuberculate, and/or muricate, winged or wingless at margin, the glochidiate marginal prickles (when present) arranged in one or more rows, confluent at their bases to form a cupulate border [or not confluent], the ventral (adaxial) side keeled; attachment scars very narrow, extending along the keel; gynobase subulate, nearly as long as the nutlets, usually differentiated into winglike extensions between the nutlets; style persistent, concealed between the apices of nutlets [or exerted well above them]. Base chromosome numbers 11, 12. (Including *Echinosperrum* Sw., *Sclerocaryopsis* Brand, *Staurina* Nutt.) TYPE SPECIES: *L. Myosotis* Moench = *Myosotis Lappula* L. = *L. squarrosa* (Retz.) Dumort. (Generic name a diminutive of Latin *lappa*, a bur.) — STICKSEED, BURSEED.

A taxonomically difficult genus of about 40 species with the center of greatest diversity in central Asia and western Siberia, and only a few species endemic elsewhere. Wang (1981) recognized 31 species

(11 endemic) in China alone, but the status of many of these requires critical evaluation. Numerous authors have indicated that *Lappula* is represented by endemic species in Australia, southern Africa, and North America, but Popov showed that those taxa belong either to other genera or are conspecific with Asiatic members of *Lappula*. The genus is represented in the New World by two species that are definitely native to Central Asia and at least one of which has both indigenous and naturalized populations in North America. Both of these species have been recorded from the southeastern United States.

Lappula squarrosa (Retz.) Dumort. (*Myosotis squarrosa* Retz., *Echinosperrum sgarrosum* (Retz.) Reichenb., *M. Lappula* L., *L. Lappula* (L.) Karsten, *L. Myosotis* Moench, *E. Fremontii* Torrey, *L. Fremontii* (Torrey) Greene, *L. erecta* A. Nelson, *L. echinata* Gilibert¹⁰), $2n = 48$, is widespread in Canada and the western and central United States. It is apparently very rare in the Southeast, where it has been reported from Tennessee (Rogers & Bowers; Small, 1933) and possibly Arkansas (Smith, 1978).

Lappula Redowskii (Hornem.) Greene (*Myosotis Redowskii* Hornem., *Echinosperrum Redowskii* (Hornem.) Lehm., *E. texanum* Scheele, *L. texana* (Scheele) Britton; *L. Redowskii* var. *texana* (Scheele) Brand; see Cronquist and Johnston (1932) for some 50 additional synonyms), $2n = 48$, is a Eurasian and western North American weed that usually grows in disturbed areas such as roadsides, abandoned fields, pastures, and waste places. It is widespread in Canada and the central and western United States but is very rare and apparently introduced in Arkansas (Smith, 1988).

Lappula Redowskii is readily distinguished from *L. squarrosa* in having nutlets with one row of glochidiate marginal prickles that are often confluent at their bases. In contrast, in *L. squarrosa* the nutlets have two or three rows of marginal prickles that are distinct at the base.

Lappula Redowskii is perhaps the most variable species in the genus, and many of its morphological extremes have been variously recognized at the rank of species, subspecies, varietas, or forma. Two commonly occurring extremes that are connected by a wide array of intermediates are present in North America. For practical purposes, these extremes are recognized here at the varietal rank. In var. *Redowskii* the marginal prickles of the nutlets are distinct, whereas in var. *cupulata* (A. Gray) M. E. Jones the prickles are connate at base to form a cup-shaped margin. The latter variety was treated by Johnston (1924) and Johnston *et al.* as a distinct species, *L. texana*, but the connation of the lateral prickles can be so variable within a given population (or sometimes even on the same plant) that it is doubtfully useful in subdividing the species.

¹⁰*Lappula squarrosa* is better known as *L. echinata* Gilibert in most treatments, including those of Fernald, Gleason, Johnston (1924), Johnston *et al.*, and Popov (1953). Under the present International Code (ICBN, Article 23, Example 11. 1988), however, Gilibert's names should not be considered for specific epithets because he (Fl. Lithuan. 1781) did not consistently employ the Linnaean system of binary nomenclature.

Johnston's statement (1927, p. 101) that *Lappula* is "a very difficult genus" has been confirmed by various students of the Boraginaceae. Species of the genus are distinguished from each other almost exclusively on the basis of fruit characters. Nutlet shape, size, and sculpture, as well as the nature of the abaxial (dorsal) margin have been emphasized. Edmondson's suggestion that environmental modifications of nutlet morphology and the role of hybridization in obscuring species boundaries should be critically evaluated is quite appropriate. Although an accurate determination of the number of species in *Lappula* is not yet possible, Higgins's estimate of ten species in the genus is well below the mark, while Johnston's (1924) recognition of six species and eight varieties in North America is probably exaggerated. It is most likely that only two polymorphic species of *Lappula* are present in the New World.

Although there is some agreement among students of *Lappula* in regard to the number of sections, the subsectional classification of the genus is controversial and needs critical study. Two of De Candolle's three sections of *Lappula* (as *Echinospermum*) are now maintained in the genus. The third, sect. *Homalocaryum* DC., is now treated in *Hackelia* Opiz. Gürke added a fourth section, but this is generally accepted as a well-defined genus, *Heterocaryum* DC., assigned to a subtribe of the family different from that containing *Lappula* (Riedl). Section SCLEROCARYUM DC. (nutlets not marginate, adnate to a gynophore with a reduced column) is primarily Asian and includes a few species, none of which occurs in the New World. Section LAPPULA (nutlets marginate, usually prickly, readily separable from a gynophore that has a well-developed column) contains the bulk of the genus, including the two North American representatives. This last section has been divided by Popov (1953) into 11 series and by Wang (1981) into seven subsections. *Lappula squarrosa* belongs to subsect. *Lappula* (nutlets with two or three rows of marginal prickles), whereas *L. Redowskii* belongs to subsect. *Macranthae* (Popov) Riedl (nutlets pyramidal, with one row of marginal prickles).

Lappula is somewhat related to *Hackelia*, from which it is distinguished by several characters listed under the latter. It differs from *Heterocaryum* (six species, western Asia) in having more or less equal, ovoid, usually triangular nutlets that are attached ventrally to an elongated, narrow gynophore. In contrast, *Heterocaryum* has unequal, oblong to linear nutlets connate to each other and adnate to the gynophore.

The reproductive biology of *Lappula* is poorly understood. Owing to their small, inconspicuous flowers, species of the genus apparently are largely inbreeders. The flowers of *L. squarrosa* are self-compatible, and the plant is primarily autogamous (Frick).

Chromosome numbers have been reported for only eight species (about 20 percent of the total). *Lappula microcarpa* (Ledeb.) Gürke and *L. tadishkorum* Popov are diploid, $2n = 22$ (Huss, Vasudevan). The other six are tetraploids based on 12. The report by Taylor &

Mulligan of $n = 23$ for *L. squarrosa* (as *L. echinata*) needs verification because numerous other populations have been found to have $2n = 48$. Furthermore, *L. barbata* (Bieb.) Gürke apparently has diploid ($2n = 24$) populations (Bolkhovskikh *et al.*), as well as tetraploids ($2n = 48$) reported by other workers.

Pollen of *Lappula* is dumbbell shaped, 6-heterocolporate, and heteropolar. The three pseudocolpi are long and narrow, and they alternate with three short colporate apertures that widen toward the equator (Ahn & Lee; Clarke; Sahay).

Pyrrrolizidine alkaloids have been analyzed for only *Lappula Redowskii* (as *L. intermedia* (Ledeb.) Popov), in which Smith & Culvenor found lasiocarpine. The fatty acids of *L. heteracantha* (Ledeb.) Borb., *L. Redowskii*, and *L. squarrosa* have been studied by Kleiman *et al.* and Tétényi. All three species contain some amounts of linolenic (26–32 percent), oleic (18–27 percent), and linoleic (16–20 percent) acids. The scant chemical data do not show patterns of chemotaxonomic significance.

Nutlets of *Lappula* are dispersed almost exclusively by animals. The presence of one or more rows of glochidiate prickles at the dorsal margin of the nutlet are adaptations to such dispersal.

Lappula Redowskii has been used by the Navajo Indians to prepare an infusion used as a lotion for swellings and sores, and the roots of *L. squarrosa* (as *Echinosperrum Lappula*) were used by Ojibwa Indians as a snuff or inhalant for headache (Moerman). Several species of the genus are noxious weeds, and the fleece of sheep can become densely matted with nutlets (Frick).

REFERENCES:

- Under family references see AHN & LEE; AL-NOWAIHI *et al.*; BAILLON; BOLKHOVSKIKH *et al.*; BRAND (1915b); BRITTON; BULL *et al.*; DE CANDOLLE; G. C. S. CLARKE; CRONQUIST (1984); FEDOREEV & KRIVOSHCHEKOVA; FERNALD; GATTINGER; GLEASON; GOLDBLATT (1981, 1984, 1985, 1988); GREENE; GÜRKE; HEGI; HIGGINS (1979); HILGER (1985); HOFFMANN *et al.*; JOHNSTON (1923, 1924a, 1927, 1932); JOHNSTON *et al.*; KLEIMAN *et al.*; MITCHELL & ROOK; MOERMAN; R. J. MOORE (1973, 1977); MUENSCHER; ORNDUFF (1969); PARK; RIEDL (1967); SAHAY; SCHAEFER; SMALL (1933); E. B. SMITH (1978, 1988); SMITH & CULVENOR; STEYERMARK; STREY; TÉTÉNYI; VASUDEVAN; VOYTENKO & OPARINA (1985, 1987); and WILLAMAN & LI.
- BRAND, A. *Lappula*. In: A. ENGLER, ed., Pflanzenreich IV. **252**(Heft 97): 136–155. 1931. [Fourteen species.]
- CHATER, A. O. *Lappula*. In: T. G. TUTIN *et al.*, eds., Fl. Europaea **3**: 117, 118. 1972. [Six species recognized; *Hackelia* reduced to synonymy of *Lappula*.]
- EDMONDSON, J. R. *Lappula*. In: P. H. DAVIS, ed., Fl. Turkey **6**: 255–261. 1978. [Seven species; brief note on diversity and some taxonomic difficulties within the genus.]
- FRICK, B. The biology of Canadian weeds 62. *Lappula squarrosa* (Retz.) Dumort. Canad. Jour. Pl. Sci. **64**: 375–386. 1984. [Description, economic importance, distribution, habitats, growth and development, reproductive biology.]

- HOLUB, J. *Lappula patula* (Lehm.) Menyh., a new casual in the Czechoslovak flora. (In Czech; English summary.) *Preslia* **46**: 333-342. 1972. [Description, synonymy, infraspecific taxa, distinguishing characters, key.]
- HUSS, H. Karyologische Studien an Samenpflanzen aus dem Wakhan und Grossen Pamir (NO-Afghanistan), I. (English summary.) *Phyton Austria* **21**: 1-24. 3 pls. 1981. [*L. tadishkorum*, 5, $n = 11$, $2n = 22$.]
- KUDABAEVA, G. M. De genere *Lappula* Moench notula. (In Russian.) *Bot. Mater. Gerb. Inst. Bot. Akad. Nauk. Kazakh SSR* **13**: 60-63. 1983.* [Related papers in *Ibid.* **58**, **59**, and **12**: **47**, **48**. 1982.*]
- POPOV, M. Boraginaceae novae. (In Russian.) *Notul. Syst.* **14**: 305-335. 1951. [*Lappula*, 311-333; eleven species, five new; illustrations.]
- . *Lappula*. In: B. K. SHISHKIN, ed., *Fl. USSR* **19**: 403-479. 1953. English translation by R. LAVOOTT, **19**: 300-356. 1974. [Thirty-nine species; sectional classification, detailed descriptions and taxonomic notes.]
- RAENKO, L. M. The genus *Lappula* Moench of Turkmenistan flora. (In Russian; English summary.) *Izv. Akad. Nauk. Turkm. SSR, Biol. Nauk.* **1985**(5): 19-25. 1985. [Eleven species; key, descriptions, synonymy, distributions.]
- . New taxa of the family Boraginaceae from Turkmenia. (In Russian.) *Bot. Zhur.* **72**: 98-100. 1987. [*L. Nevskii*, sp. nov.]
- RIEDL, H., & M. IRANSHAHR. A new species of *Lappula* from Iran, with notes on the infrageneric division of the genus. *Linzer Biol. Beitr.* **17**: 327-332. 1985. [*L. semnanensis*, sp. nov.; notes on some members of series *Sinaicae*, variation in the *L. sinaica* complex.]
- ROGERS, K. E., & F. D. BOWERS. Notes on Tennessee plants III. *Castanea* **38**: 335-339. 1973. [*L. squarrosa* (as *L. echinata*) in Shelby County, 338.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez l'*Echinosperrum Lappula* Lehm. *Compt. Rend. Acad. Sci. Paris* **247**: 761-766. 1958. [*L. squarrosa*.]
- TAYLOR, R. L., & G. A. MULLIGAN. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. 148 pp. Ottawa, Canada. 1968. [*L. squarrosa* (as *L. echinata*), 101, $n = 23$.]
- WANG, C.-J. Two new species of *Lappula* Wolf (Boraginaceae) from Xizang (Tibet). *Acta Phytotax. Sinica* **18**: 521, 522. 1980. [*L. caespitosa* and *L. himalayensis*, spp. nov.]
- . A study on the genus *Lappula* of China. (In Chinese; English summary.) *Bull. Bot. Res. North-East Forest. Inst.* **1**(4): 77-100. 1981. [Thirty-one species in two sections and seven subsections; nine species, five varieties and four subsections described as new.]
- WANG, X.-C., Y.-H. PEI, X. LI, & T.-R. ZHU. Studies on the antibacterial constituents in the fruit of *Lappula echinata*. *Acta Pharm. Sinica* **21**: 183-186. 1986.* [*L. squarrosa*.]

Tribe 3. CYNOGLOSSEAE DC. in Meisner, Comm. Götting.
187. 1836-1843.

11. *Cynoglossum* Linnaeus, Sp. Pl. 1: 134. 1753; Gen. Pl. ed. 5. 65. 1754.

Perennial, biennial [or rarely annual], hirsute to hispid or strigose [rarely glabrous] herbs. Stems erect, hollow, simple at base, usually branched above. Basal leaves long-petiolate, rosulate, persistent or withering; cauline leaves alternate, sessile, usually amplexicaul. Inflorescences densely flowered, ebracteate [or bracteate], usually terminal

cymes, often paniculate [or subcapitate], usually elongating considerably in fruit. Calyx 5 lobed, often deeply divided to the base, persistent, accrescent [or not] and stellately spreading to reflexed in fruit. Corolla funnellform [subrotate or nearly tubular], blue, white, purplish [or red]; lobes imbricate, broad, spreading; throat with 5 trapeziform, subquadrate, or rarely oblong to lunate faucal appendages, these included and usually closing the throat, entire to emarginate at apex, glabrous or papillose; tube short [or long]. Stamens 5, included, filaments shorter than anthers, inserted in corolla tube; anthers oblong to ovoid, not appendaged. Ovary deeply 4 lobed, 4 ovulate; style gynobasic, persistent, shorter than corolla; stigma capitate. Nutlets 4 (rarely fewer by abortion), depressed ovoid to suborbicular, glochidiate all around or only dorsally, dorsiventrally compressed or not, wingless, with or without an elevated margin or rim, free or coherent to style and sometimes at maturity splitting from it bearing an arista (a stiff bristle) of styler tissue; attachment scar medial to apical; gynobase narrowly conical. Base chromosome number 12. (Including *Paracynoglossum* Popov.) LECTOTYPE SPECIES: *C. officinale* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. 3: 75. 1913. (Name from Greek *cynos*, of a dog, and *glossa*, tongue, from the texture and shape of the leaves.) — HOUND'S TONGUE, BEGGAR'S LICE.

A cosmopolitan genus of about 75 species distributed primarily in Eurasia and Africa, with a poor representation in North America (ten species; seven indigenous). Of the four species that occur in the southeastern United States, only one is indigenous.

Subgenus CYNOGLOSSUM (corolla large to medium sized; faucal appendages large, entire, not emarginate; nutlets relatively large [more than 3 mm long], coherent to style and separating from it bearing an arista) includes two sections, of which one, sect. CYNOGLOSSUM (inflorescence ebracteate, nutlets marginate or immarginate), is represented in the Southeastern States by the following two species.

Cynoglossum virginianum L. (*C. amplexicaule* Michx., *C. lucidum* Stokes), wild comfrey, $2n = 24$, is indigenous to the United States, where it is distributed from southern Connecticut south into Florida, west into Texas, Missouri, and Illinois. It is found in all of the Southeastern States and grows along roadsides and in deciduous woods, meadows, and thickets. It is a perennial with few cymes held well above the amplexicaul stem leaves by a distinct peduncle, large calyces (3.4–4.5 mm), broad corollas (1–1.2 cm wide), and dorsally rounded nutlets (5.5–7 mm long). It is most closely related to *C. boreale* Fern., a species recognized as distinct by Johnston (1924a), who suggested (p. 34) that "it is deserving of varietal rank at the very least," and reduced by Brand to the synonymy of *C. virginianum*. The basic difference between the two is that *C. boreale*, which grows in the northern United States and adjacent southern Canada, has smaller (2–2.5 mm) calyces, narrower (6–8 mm) corollas, and smaller (3.5–4.5 mm) nutlets (Fernald). Mill

placed the two species in subg. *Eleutherostylum* (Brand) Riedl, which he raised to generic rank.

Cynoglossum officinale L., hound's tongue, $2n = 24, 28$, is a Eurasian weed naturalized in North Carolina, Georgia, Tennessee, Alabama, and Arkansas. It grows in pastures, waste places, and fields, as well as along roadsides. Several authors (e.g., Duncan & Kartesz; Small (1933); Steyermark) have reported it from Georgia, but Jones & Coile did not include it in their county distributions. The species is readily distinguished from other members of the genus in the Southeast by being a biennial caescent with soft, fine hairs and in having stems leafy to the inflorescence and nutlets dorsally compressed and with a well-developed rim.

Subgenus PAPILLIGERUM Riedl (faucal appendages emarginate to 2-lobed, papillose on entire surface) is represented in the Southeast by *Cynoglossum amabile* Stapf, $2n = 24$, a species indigenous to China and India and reported to be naturalized in Arkansas (Smith, 1978, 1988).

Subgenus PARACYNOGLOSSUM (Popov) Riedl (corollas small; faucal appendages entire; nutlets free from style, not separating with an arista) includes two sections, of which sect. PARACYNOGLOSSUM (cymes terminal, ebracteate) is represented in the Southeastern States by a single species. *Cynoglossum zeylanicum* (Vahl) Thunb. ex Lehm. (*C. furcatum* Wall. ex Roxb.), $2n = 24$, a native of central, eastern and southeastern Asia, is very rare in Louisiana (MacRoberts) and central Florida, where it was reported as *C. furcatum* (Ward & Fantz; Wunderlin). It is easily distinguished from the species above by its small (2.5–3.5 mm), emarginate nutlets, softly-pilose leaves, and transversely oblong faucal appendages.

The generic limits and infrageneric classification of *Cynoglossum* have been and still are controversial. Johnston (1924b) adopted a broad generic concept and reduced to the synonymy of *Cynoglossum* (but without proposing new combinations) the genera *Adelocaryum* Brand (now *Brandella* R. Mill), *Trachelanthus* Kunze, *Lindelofia* Lehm., and *Solenanthus* Ledeb. He also merged *Anchusopsis* Bisch. and *Kuschakewiczia* Regel & Smirnov with *Cynoglossum*, but these are generally considered to be synonyms of *Lindelofia* and *Solenanthus*, respectively. A generic concept much broader than Johnston's (1924b) has been recently proposed by Greuter & Burdet, who made 43 new nomenclatural combinations to accommodate the transfer to *Cynoglossum* of taxa generally placed in the genera *Paracaryum* (DC.) Boiss. (including *Mattiastrum* Brand), *Pardoglossum* Barbier & Mathez, *Rindera* Pallas, *Solenanthus*, and *Trachelanthus*. A very narrow concept of *Cynoglossum* was adopted by Popov and by Mill, who narrowed the genus to include only about 17 species. In my opinion both the very broad and very narrow generic concepts of *Cynoglossum* are unacceptable, and a conservative, traditional concept, which follows Riedl (1962, 1976), is adopted here.

Cynoglossum is readily distinguished from the closely related Eurasian *Solenanthus* (ca. 17 species) and *Trachelanthus* (3 species) in having included, instead of exserted stamens; from *Lindelofia* (11 species) in having corollas subrotate to broadly funnelform and with short tubes, instead of cylindrical corollas with long tubes; from *Pardoglossum* (6 species) in having slender, glabrous glochids on the nutlets, instead of swollen glochids that are densely covered with minute papillae; and from *Paracaryum* (ca. 70 species) and *Rindera* (ca. 25 species) in having wingless, instead of winged nutlets.

All of the 25 species of *Cynoglossum* that have been surveyed cytologically are diploid, $2n = 24$. *Cynoglossum hungaricum* Simk. and *C. officinale* also have tetraploid populations. The karyotypes of six species have been studied, and the cytological data on the genus have been reviewed by Luque & Valdés.

Natural hybridization between *Cynoglossum officinale* and *C. germanicum* Jacq. has been reported from Austria, Czechoslovakia, and Romania (Stace), as well as between some members of the *C. montanum* L. complex (Mill).

In the endosperm development (Tokć, Khaleel) in *Cynoglossum officinale* and *C. glochidiatum* Wall. (as *C. denticulatum* A. DC.) the primary endosperm nucleus divides into two nuclei that either remain free or become separated by a transverse wall. The subsequent division of these nuclei leads to the formation of a micropylar cellular chamber and a chalazal nuclear chamber.

Many species of *Cynoglossum* have been surveyed palynologically. The pollen is dumbbell shaped and 6-heterocolpörate, with the three colporate apertures connected at the equator by transverse arms to three longer, alternating pseudocolpi (Clarke). Pollen morphology is very useful in distinguishing *Cynoglossum* from the closely related *Pardoglossum* (Barbier & Mathez).

The fatty-acid composition of a few species of *Cynoglossum* has been studied, and the scant data indicate that oleic acid and linoleic acids are the principal constituents, whereas linolenic acid is present in much smaller concentrations (Kleiman *et al.*, Tétényi). The pyrrolizidine alkaloids of the nine species surveyed show some interesting patterns of potential chemotaxonomic value (Smith & Culvenor), but many more species need to be analyzed before useful conclusions are reached.

The nutlets of *Cynoglossum* are covered with numerous glochidiate prickles and are dispersed by clinging to the fur of animals. Ridley observed that in England plants of *C. montanum* and *C. officinale* are abundant at the mouth of rabbit burrows, where the animals sit and clean their fur. He also noted that the tropical species of *Cynoglossum* generally have smaller nutlets than those of the temperate areas, and that small nutlets are sometimes dispersed by birds. A single plant of *C. officinale* produces an average of 297 nutlets, each weighing about 30 mg (Boorman & Fuller), and the fruits are often transported adhering to human clothing.

Some species of *Cynoglossum* (e.g., *C. officinale*) are noxious weeds that are reported to cause livestock poisoning in Europe. Medicinal values have been attributed to various species (Mitchell & Rook; Moerman; Uphof). Some are cultivated as ornamentals (see Bailey *et al.*).

REFERENCES:

- Under family references see AHN & LEE; AL-NOWAIHI *et al.*; ALTAMURA *et al.*; BACIU; BAILEY *et al.*; BAILLON, BARBIER & MATHEZ; BENTHAM & HOOKER; BOL-KHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; H. M. BURKILL; DE CANDOLLE; CHAPMAN; G. C. S. CLARKE; CLEWELL; Díez (1984); DUKE & AYENSU; DUNCAN & KARTESZ; FABRE; FEDOREEV & KRIVOSHCHIEKOVA; FERNALD; FERNANDES & LEITÃO; GATTINGER; GLEASON; GOLDBLATT (1981, 1984a, b, 1988); GÜRKE; GUPTA; HEGI; HIGGINS (1979); HILGER (1981a, b, 1985); HOFMAN *et al.*; HOMMERSAND; HUNTER; ISHIKURA; JODIN; JOHNSTON (1924a, b, 1927); JOHNSTON *et al.*; JONES & COILE; KERNER VON MARILAUN; KNUTH; LEWIS & ELVIN-LEWIS; LUBBOCK; MACROBERTS; MARTINS; MILL (1979, 1989); J. S. MILLER (1988); MITCHELL & ROOK; MOERMAN; MOHR; R. J. MOORE (1973, 1974, 1977); MUENSCHER; NASH & MORENO; NOWICKE; ORNDUFF (1967, 1969); POPOV (1953); RICKETT; RIDLEY; RIEDL (1967, 1971); SAHAY; SCHAEFER; SHARP *et al.*; SMALL (1903, 1933); E. B. SMITH (1978, 1988); L. B. SMITH; SMITH & CULVENOR; STACE; STEYERMARK; STREY; SYNGE; TAYLOR; TÉTÉNYI; UPHOF; WARD & FANTZ; WILLAMAN & LI; WILLAMAN & SCHUBERT; WUNDERLIN; and ZALKOW *et al.*
- BOORMAN, L. A., & R. M. FULLER. The comparative ecology of two sand dune biennials: *Lactuca virosa* L. and *Cynoglossum officinale* L. *New Phytol.* **96**: 609–629. 1984. [Seed production, germination, dormancy, dispersal.]
- BRAND, A. Boraginaceae-Boraginoideae-Cynoglosseae. *In*: A. ENGLER, ed., *Pflanzenreich IV*. **252**(Heft 78): 1–183. 1921. [*Cynoglossum*, 114–153; 48 species in two sections.]
- BREEMEN, A. M. M. VAN. Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* **33**: 283–305. 1984. [Effects of temperature, moisture, and light on seed germination of *C. officinale*.]
- & B. H. VAN LEEUWEN. The seed bank of three short-lived monocarpic species, *Cirsium vulgare* (Compositae), *Echium vulgare* and *Cynoglossum officinale* (Boraginaceae). (Abstr.) *Ibid.* **32**: 245, 246. 1983. [Seed survival within 13 populations of *C. officinale* for four years.]
- CRÉTÉ, P. Embryogénies des boragacées. Développement de l'embryon chez le *Cynoglossum officinale* L. *Compt. Rend. Acad. Sci. Paris* **241**: 660–662. 1955. [Stages of embryogeny from zygote to differentiation in embryo.]
- CROWLEY, H. C., & C. C. J. CULVENOR. Alkaloids of *Cynoglossum latifolium* R. Br. Latifoline and 7-angelylretronecine. *Austral. Jour. Chem.* **15**: 139–144. 1962.
- CULVENOR, C. C. J., & L. W. SMITH. The alkaloids of *Cynoglossum australe* R. Br. and *C. amabile* Stapf & Drummond. *Austral. Jour. Chem.* **20**: 2499–2503. 1967. [*C. australe* contains cynaustaline and cynaustine; *C. amabile* contains echinatine and amabiline.]
- DE JONG, T. J., & P. G. L. KLINKHAMER. Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand-dune area. *Jour. Ecol.* **76**: 366–382. 1988a. [Demographic study of 90 populations observed in plots for three years; seedling survival, density, predation.]
- & ———. Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: the importance of water for differential survival and growth. *Ibid.* 393–402. 1988b.

- , ———, A. H. GERITZ, & E. VAN DER MEIJDEN. Why biennials delay flowering: an optimization model and field data on *Cirsium vulgare* and *Cynoglossum officinale*. *Acta Bot. Neerl.* **38**: 41–55. 1989. [Demography, population growth rate, minimum size of plant for flowering.]
- , ——— & A. H. PRINS. Flowering behavior of the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **103**: 219–229. 1986. [Flowering depends on plant size; vernalization, delay of flowering, flower induction.]
- ESPINAR, L. A. *Cynoglossum amabile* (Boraginaceae) en el centro de Argentina. (English summary.) *Kurtziana* **17**: 145–148. 1984. [Description, illustration, differences from *C. creticum*.]
- FREIJSEN, A. H. J. Some experiments on the calcicolous plant *Cynoglossum officinale* L. *Verh. Nederl. Akad. Wet.* **2**: 66: 97–99. 1975. [Effects of calcium content in soil on germination and growth.]
- . Germination and culture experiments with calcareous and acid dune-sand substrates on the calcicolous *Cynoglossum officinale* L. *Ibid.* **67**: 138–140. 1976. [Effects of pH on seed germination.]
- , S. R. TROELSTRA, & M. J. VAN KATS. The effects of soil nitrate on the germination of *Cynoglossum officinale* L. (Boraginaceae) and its ecological significance. *Acta Oecol.* **1**: 71–79. 1980. [Seed germination enhanced in calcareous soils rich in nitrate.]
- GREUTER, W., & H. M. BURDET. In: W. GREUTER, ed., *Med-checklist notulae*, 3. *Willdenowia* **11**: 23–43. 1981. [*Cynoglossum*, 32–36; 43 new combinations proposed.]
- HIGGINS, L. C. A new name for *Cynoglossum erectum* (Boraginaceae). *Phytologia* **34**: 234. 1976. [*C. Henricksonii* Higgins replaces the later homonym *C. erectum* Higgins, a species endemic to the Chihuahuan desert; see *Ibid.* **33**: 411. 1976.]
- KHALEEL, T. F. Embryology of *Cynoglossum denticulatum* DC. *Bot. Not.* **127**: 193–210. 1974. [Anther development, micro- and megasporogenesis, embryogeny, anatomy of seed coat and pericarp, development of glochidiate spines; see MILLSAPS and TOKČ.]
- KLINKHAMER, P. G. L., & T. J. DE JONG. Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **106**: 773–783. 1987. [Seed number increased proportionally with plant size.]
- & ———. The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. *Jour. Ecol.* **76**: 383–392. 1968. [Germination, mortality, effects of disturbance.]
- KOVANDA, M. *Cynoglossum*. In: T. G. TUTIN, et al., eds., *Fl. Europaea* **3**: 119–121. 1972. [Eleven species.]
- LHOTSKÁ, M. Beitrag zur Keimungsökologie und Diasporologie der tschechoslowakischen Vertreter der Gattung *Cynoglossum*. (English summary.) *Folia Geobot. Phytotax.* **17**: 269–293. 1982. [Three species; dormancy, seed germination, stratification, dispersal, habitats.]
- LIU, Y.-L. New taxa of *Cynoglossum* L. from China. *Acta Phytotax. Sinica* **19**: 519, 520. 1981. [*C. gansuense*, sp. nov., and a new variety of *C. amabile*.]
- LUDLOW-WIECHERS, B., & R. PALACIOS-CHÁVEZ. Catálogo palinológico para la flora de Veracruz. No. 24. Familia Boraginaceae. Género *Cynoglossum*. (English summary.) *Biotica* **10**: 277–290. 1985. [*C. amabile*; pollen tetrazonocolporate, with a thin exine, and psilate.]
- LUQUE, T., & B. VALDÉS Caryological study of Spanish Boraginaceae III. *Cynoglossum* L. s. str. *Willdenowia* **15**: 485–496. 1986. [Eight taxa; karyotypes, review of earlier chromosome counts for the genus.]
- MANKO, I. V. Analysis of the alkaloids of *Cynoglossum*. II. *C. officinale* L. (In Russian.) *Ukrain. Khim. Zhur.* **25**: 627–630. 1959.*
- . Study of alkaloids of *Cynoglossum amabile* Stapf et Drumm. & *Cynoglossum viridiflorum* Pall. ex Lehm. (In Russian.) *Rastitel Resursy* **8**: 243–246. 1972.*

- & L. G. MARCHENKO. A study of the alkaloids of *Cynoglossum pictum*. Chem. Nat. Compounds 7(5): 66. 1971.*
- MATTHEWS, J. F., & T. L. MELLICHAMP. Additional records to the vascular flora of the Carolinas and a selected bibliography of floristic studies, 1964–1987. Jour. Elisha Mitchell Sci. Soc. 105: 34–54. 1989. [*C. virginianum* in Caldwell County, North Carolina, 42.]
- MILL, R. R., & A. G. MILLER. Studies in the flora of Arabia: IX. A synopsis of *Paracynoglossum* (Boraginaceae). Notes Bot. Gard. Edinburgh 41: 473–482. 1984. [New taxa, distributions, key, maps; genus reduced to a section of *Cynoglossum*; see MILL (1989).]
- MILLSAPS, V. Structure and development of the seed of *Cynoglossum amabile* Stapf & Drumm. Jour. Elisha Mitchell Sci. Soc. 56: 140–164. pls. 4–6. 1940. [Anther development, microsporogenesis, pollen, chromosome number, ovule anatomy, megasporogenesis, embryogeny; see KHALEEL and TOKĆ.]
- PASLAWSKA, S. Kinetics of the extraction of silicon compounds from the leaves of *Cynoglossum officinale*. Ann. Acad. Med. Gedanensis 10: 355–362. 1980.*
- PEDERSEN, E. Minor pyrrolizidine alkaloids from *Cynoglossum officinale*. Dansk. Tidsskr. Farm. 44: 287–291. 1970.*
- PITOT, A. Le fruit du *Cynoglossum pictum*, Boraginacée. Bull. Soc. Bot. France 87: 256–260. 1940. [Description, anatomy.]
- RIEDL, H. Bemerkungen über *Cynoglossum coelestinum* Lindl. und *C. glochidiatum* Wall. sowie Versuch einer Neugliederung der Gattung *Cynoglossum* L. Österr. Bot. Zeitschr. 109: 385–394. 1962. [*Cynoglossum* divided into four subgenera and seven sections.]
- . *Cynoglossum*. In: P. H. DAVIS, ed., Fl. Turkey 6: 306–311. 1978. [Seven species recognized; problems of generic limits.]
- . New species and combinations of Cynoglosseae from Ethiopia. Linzer Biol. Beitr. 17: 317–325. 1985. [*C. alpinum*, *C. Hedbergiorum*, spp. nov.; *Paracynoglossum* recognized as a subgenus of *Cynoglossum*; *C. afrocaeruleum*, comb. nov.]
- SAITO, K. Studies on inducing polyploid flower plants and their utilization. II. On several polyploid plants of *Cynoglossum*, *Coreopsis*, *Dianthus* and others. (In Japanese; English summary.) Jour. Hort. Assoc. Japan 19: 107–112. 1950.*
- STACE, C. A. *Cynoglossum*. P. 353 in C. A. STACE, Hybridization and the flora of the British Isles. London, New York, and San Francisco. 1975. [*C. germanicum* × *C. officinale*.]
- STARCHENKO, V. M. The genus *Cynoglossum* in the Soviet Far East. (In Russian.) Bot. Zhur. 63: 1030–1032. 1978. [Brief notes on certain species.]
- SURI, K. A., P. G. RAO, R. S. SAWHNEY, & C. K. ATAL. Pyrrolizidine alkaloids from *Cynoglossum zeylanicum* and *Cynoglossum lanceolatum*. Indian Jour. Pharm. 35: 20. 1973.*
- TACINA, F. The optical and electron microscopic structure of the nectariferous gland in *Cynoglossum officinale*. Rev. Roum. Biol. Bot. 18: 201–209. 1973.*
- TOKĆ, E. Endosperm and embryo development in *Cynoglossum officinale* L. Acta Biol. Cracov. Bot. 19: 47–58. pl. 6. 1976. [Endosperm development markedly differs from that reported earlier for *C. amabile* and *C. denticulatum*; see KHALEEL and MILLSAPS.]
- WOFFORD, B. E., T. S. PATRICK, L. R. PHILLIPPE, & D. H. WEBB. The vascular flora of Savage Gulf, Tennessee. Sida 8: 135–151. 1979. [*C. virginianum* in Grundy County, 144.]
- WRABER, T. Ein neues *Cynoglossum* (*C. Krasnigii*) aus Jugoslawien. (English summary.) Candollea 41: 145–150. 1986. [Illustration, photographs, relationships.]

Tribe 4. LITHOSPERMEAE (DC.) Gürke in Engler & Prantl,
Nat. Pflanzenfam. VI. 3A: 118. 1879.

12. *Lithospermum* Linnaeus, Sp. Pl. 1: 132. 1753; Gen. Pl. ed. 5. 64. 1754.

Perennial [or rarely annual] herbs, usually with taproots or rootstocks containing a red pigment; stems erect or spreading. Leaves entire, alternate, sometimes forming sterile basal clusters. Cymes scorpioid, bracteate, considerably elongated in fruit; flowers homostylous or heterostylous, sometimes cleistogamous; infructescences racemelike; bracts foliaceous, usually longer than the fruiting calyx. Calyx usually 5 parted, the lobes linear to lanceolate. Corolla yellow, orange [white, pinkish, or bluish], funnelform, salverform [or cylindric], pubescent on the outside; corolla lobes spreading, equal, or nearly so, imbricate in bud, entire or lacerate to erose at margin; corolla tube straight, often gradually enlarging above the middle; throat with or without faucal appendages, usually bearing small stipitate glands; annulus usually hairy. Stamens 5, included, arising above the middle of the corolla tube or (in long-styled flowers) below the middle, shorter than the anthers; anthers oblong, obtuse or apiculate at apex. Ovary 4 lobed; style slender, usually included; stigmas 2, distinct, globose to ellipsoid. Nutlets 4 (or fewer by abortion), erect, ovoid or ellipsoid, smooth and porcelain-like or rugose to somewhat pitted, very hard and bonelike; attachment scar large, basal, plane or convex; gynobase flat to broadly pyramidal. Seeds straight; cotyledons flat. Base chromosome numbers 7, 10–13. (Including *Batschia* Gmelin, *Cyphorima* Raf., *Pentalophus* A. DC.) LECTOTYPE SPECIES: *L. officinale* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. 3: 87. 1913. (Name from Greek *lithos*, stone, and *sperma*, seed, from the hard, stonelike nutlets.)—GROMWELL, PUCCOON, STONESEED.

A genus of about 45 species distributed on all continents except Australia and Antarctica, with the center of greatest diversity in Mexico and the adjacent United States, where some 32 species are indigenous. Of these, nine occur in both countries, fourteen are restricted to Mexico, and six to the United States. Five species are indigenous to South America, five to Africa, three to Asia, and one each to Eurasia and Europe. The genus is represented in the southeastern United States by five indigenous species.

Lithospermum canescens (Michx.) Lehm. (*Batschia canescens* Michx., *Anchusa canescens* (Michx.) Muhl., *A. virginiana* L. (not *L. virginanum* L.), *L. sericeum* Lehm., *B. sericea* (Lehm.) Roemer & Schultes, *B. conspicua* R. Br.), Indian paint, hoary puccoon, puccoon, $2n = 14$, is distributed from southern Ontario to Saskatchewan, the Dakotas, Nebraska, and Kansas, south to Kentucky, Virginia, North Carolina, Georgia, and Alabama. It grows in sandy places, prairies, cedar glades, limestone or dolomite bluffs, and rocky ridges, as well as

along roadsides and railroads. Of the six Southeastern States in which it occurs, *L. canescens* is most widespread in Arkansas (Smith, 1988) and is apparently rare in North Carolina, where it has been reported from Durham and Granville counties (Hommersand). It has been mapped from Bartow, Catoosa, Cobb, Dade, Floyd, and Walker counties in northwestern Georgia (Jones & Coile), and I have seen material from Cherokee, Colbert, Franklin, Jackson, and Morgan counties, Alabama; Chickasaw and Lee counties, Mississippi; and Cheatham, Franklin, and Knox counties, Tennessee. Mohr reported the species from Lauderdale, Lawrence, and Madison counties, Alabama.

Lithospermum caroliniense (J. F. Gmelin) MacM.¹¹ (*Batschia caroliniensis* J. F. Gmelin, *B. Gmelinii* Michx., *L. Gmelinii* (Michx.) Hitchc.; see Johnston (1952b) and Wilbur for eight additional synonyms), puccoon, $2n = 24$ (as *L. croceum* Fern.; see Britton, 1951), grows primarily on dunes, in sandy soil of prairies, deciduous scrub or turkey oak (*Quercus laevis*) barrens, and pinelands or pine barrens, and along roadsides and railroads. It is distributed from Ontario to Michigan, Minnesota, South Dakota, Colorado, Oklahoma, Texas and adjacent Mexico in the west, and in the east southward to Ohio, Virginia, and all of the Southeastern States except North Carolina. Hommersand reported the species in Mississippi and Tennessee, but I have not seen any material from these states.

Both *Lithospermum caroliniense* and the closely related *L. canescens* are heterostylous, have showy flowers, and yield an intense red root pigment. The former is easily distinguished by its stiffly hispid leaves, orange-yellow corollas with the limb 13–25 mm wide, fruiting calyces (6–)10–17 mm long, and nutlets 3.5–4.5 mm long. In contrast, *L. canescens* has softly pilose leaves, yellow corollas with the limb 10–18 mm broad, fruiting calyces 5–6(–8) mm long, and nutlets 2–3 mm long.

Lithospermum caroliniense is highly variable in pubescence and number of leaves below the inflorescence, in venation and width of the corolla limb, and in length and flattening of calyx lobes in fruit. One of its many variants was recognized as a distinct species, *L. croceum* (Fernald, 1935; 1950, family refr.), that was reduced to subsp. *croceum* (Fern.) Cusick (1985). *Lithospermum croceum* is said to differ from *L. caroliniense* in having 30–45 leaves below the inflorescence, calyx lobes keeled in fruit, trichomes with pustular bases, and anastomosing veins of the corolla above the throat. In contrast, *L. caroliniense* is said to have fewer than 25 leaves below the inflorescence, calyx lobes flat in fruit, slender trichomes without pustular bases, and non-anastomosing veins of the corolla in the region above the throat. These differences are not well correlated, and they can be found in various combinations.

¹¹Many workers (e.g., Fernald; Johnston, 1952) have cited Walter as the author of the specific epithet. As shown by both Ward and Wilbur, however, Walter's epithet is illegitimate because it was published under the name *Anonymos* that he applied to 28 different genera (see ICBN, Article 20.4).

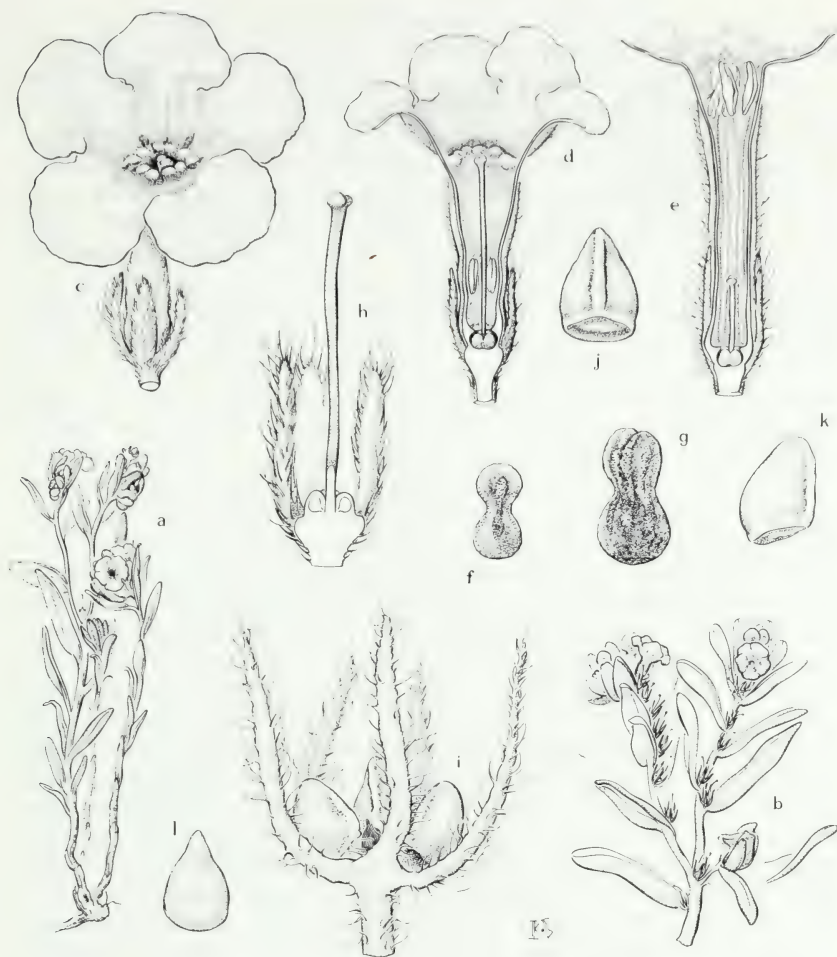


FIGURE 5. *Lithospermum*. a-l, *L. canescens*: a, flowering stem, $\times 1/2$; b, portion of inflorescence, $\times 1$; c, long-styled flower—note fornice, $\times 5$; d, vertical section of long-styled flower, $\times 10$; e, vertical section of short-styled flower, $\times 5$; f, pollen grain from long-styled flower, $\times 875$; g, pollen grain from short-styled flower, $\times 875$; h, vertical section of flower after corolla has fallen—note gynobasic style, $\times 10$; i, fruiting calyx and three of four mature nutlets, $\times 5$; j, mature nutlet seen from adaxial surface, $\times 6$; k, nutlet seen from the side, $\times 6$; l, embryo, oriented as nutlet in "j", $\times 6$.

Johnston (1952) reduced *L. croceum* to the synonymy of *L. carolinense*, stating that the differences used by Fernald to separate these species are the same that distinguish the short- and long-styled flowers of *L. caroliniense*.

Lithospermum incisum Lehm. (*L. angustifolium* Michx., *L. longiflorum* (Pursh) Sprengl, *L. linearifolium* Goldie, *Batschia linearifolia* (Goldie) Small; see Johnston (1952) and Higgins (1979) for ten

additional synonyms), $2n = 24$, is readily distinguished from the other members of the genus by its lacerate, erose, or dentate corolla lobes, recurved fruiting pedicels, linear to linear-lanceolate leaves, and in having both chasmogamous and cleistogamous flowers. Higgins (1979) and Johnston (1952) indicated that flowers produced early in the season are chasmogamous, showy, large (corollas 28–40 mm long), long-styled, and almost always sterile, whereas those produced later in the growing season are cleistogamous, inconspicuous (corollas 1–3 mm long), short-styled, and always fertile.

Lithospermum incisum is widespread in Canada (Manitoba west through British Columbia), the United States (the Mountain, Great Plains, Southwestern, and some of the Southeastern states), and northern Mexico. It grows in the Southeast from northern Florida southward into Hernando, Seminole, and Hillsborough counties (Ward & Fantz; Wunderlin), in Louisiana (MacRoberts), in western Arkansas (Smith, 1988), and in Tennessee (Chapman; Gattinger).

Lithospermum latifolium Michx. (*L. officinale* L. var. *latifolium* (Michx.) Lehm., *Cyphorima latifolia* (Michx.) Raf., *C. lutea* Raf., *L. luteum* (Raf.) House, *L. lutescens* Coleman), growwell, $2n = 28$, is an eastern North American species distributed from Ontario west to Minnesota, south into eastern Kansas and Arkansas (Newton, Pope, Garland, and St. Francis counties), east into Tennessee (Hamilton, Haywood, Marion, Sumner, and Wayne counties), Kentucky, and West Virginia, and north into Indiana and New York. It grows primarily on alluvial soil in thickets, rich woods, and in fields and along roadsides. Its nearest relative is the Eurasian *L. officinale*, $2n = 28$, 56. The latter, which is naturalized in northeastern North America (Quebec and Ontario south into Illinois and east into New Jersey, New York, and New England), was reported from Tennessee by Gattinger, but it apparently has not been recollected from that state. *Lithospermum latifolium* is easily characterized by its ovate to lanceolate leaves (1.3–)2–4.5 cm broad, corolla tubes shorter than the calyx, fruiting calyces (7–)8–14 mm long, and nutlets 3.5–5 mm long. In contrast, *L. officinale* has narrowly lanceolate leaves (0.3–)0.6–1.4(–2) cm wide, corolla tubes subequalling to slightly longer than the calyx, fruiting calyces 4–6(–8) mm long, and nutlets to 3 mm long.

Lithospermum tuberosum Rugel ex DC. is distributed primarily in the southeastern United States and is apparently restricted outside this area to Kentucky (Wayne County) and eastern Texas (Polk and Brazoria counties). It is widespread in Tennessee, Alabama, Florida, and Louisiana, less common in Georgia (Walker, Elbert, and Lee counties (Jones & Coile)) and Arkansas (Sevier, Howard, and Hempstead counties (Smith, 1988)), and very rare in South Carolina (McCormick County (Hommersand)). It has been reported from North Carolina (Rickett) and Mississippi (Hommersand), but I have not seen material from those states. *Lithospermum tuberosum* is distinct in its tuberous, fusiform roots, elliptic bracts, and well-developed rosettes of basal leaves much larger than the cauline ones.

The primarily western *Lithospermum multiflorum* Torrey in A. Gray was included in E. B. Smith's atlas of the Arkansas flora (1978), but has been omitted in the recent second edition (1988).

The limits of *Lithospermum* have been labile because most workers have followed the cumulative studies of Johnston, who changed his mind several times about the boundaries of the genus. For example, Johnston (1924) united *Buglossoides* with the earlier published *Lithospermum*, but later (1954a) he recognized them as separate genera. Johnston (1924b) also maintained both *Arnebia* Forsskål (25 species; Asia and North Africa) and *Lithospermum*, united them under the latter (1952, 1953a), and then re-separated them as distinct genera (Johnston, 1954a). He also united *Echioides* Ortega (monotypic; Armenia, Caucasus, and Iran) and *Lithospermum* (1952) but later (1954a) separated them. Students of the family now recognize *Arnebia*, *Buglossoides*, *Echioides*, and *Lithospermum* as distinct but closely related genera. *Lithospermum* is distinguished from *Arnebia* by its globose to oblong-ellipsoidal or asymmetrically constricted pollen grains with a single equatorial row of pores, as well as by its undivided styles, two stigmas, and usually stipitate glandular trichomes on the faucal appendages. In contrast, *Arnebia* has elongated pollen grains constricted at the equator into equal halves and with two rows of pores (one about each half), as well as its usually divided styles, two or four stigmas, and eglandular faucal appendages. *Echioides* is separated from *Lithospermum* by the lack of faucal appendages in the corolla and in having divided styles. The characters separating *Lithospermum* from *Buglossoides* are given under the latter. The relationships of *Lithospermum* to other closely related genera have been discussed in great detail by Johnston (1954a) and need not be repeated here.

Johnston (1952) listed 18 species of *Lithospermum* as heterostylous, but nine of those are now considered to belong to *Arnebia* and one to *Echioides*. The remaining eight, all North American, are retained in *Lithospermum*. Pollen grains of short-styled (thrum) flowers of *L. californicum* A. Gray, *L. canescens*, *L. cobrense* Greene, *L. discolor* Martens & Gal., *L. multiflorum*, *L. obovatum* Macbr., and *L. tubulifolium* Greene are larger than those of long-styled (pin) flowers, and in the last two species the grains of thrum flowers are ovate, whereas those of pin flowers are dumbbell shaped (conspicuously constricted at the middle) (Johnston, 1952). Furthermore, thrum flowers of *L. caroliniense* are larger and have larger anthers than those of pin flowers.

The association of self-incompatibility with heterostyly has been demonstrated in *Lithospermum cobrense* (Ganders) and in *L. caroliniense* (Levin, 1972). The latter species produces toward the end of the growing season some cleistogamous flowers on both pin and thrum plants. These were estimated to be up to 4.7 percent of the entire population (Levin, 1968, 1972). Cleistogamous plants were found to produce an average of 3.4 nutlets per flower, whereas chasmogamous plants produce an average of only 0.23 nutlets per flower. Levin (1968) found an excess of thrum plants in the population, but Ganders found the pin

and thrum plants in a ratio of 1:1. The report in *L. caroliniense* of binucleate pollen (Levin, 1968) is probably erroneous. Trinucleate pollen was found in *L. cobrense* (Ganders) and in various other genera of the Boraginaceae (Brewbaker), including *Lithospermum*. Johnston's conclusion (1954a) that *Lithospermum* is advanced in the Lithospermeae because of the presence of heterostyly in some of its members requires careful evaluation.

Chromosome numbers have been surveyed for only about 13 species of *Lithospermum* (about 2.6 percent of the genus). *Lithospermum canescens* is diploid with $2n = 14$, and five others are tetraploids based on seven. In *L. officinale* both tetraploid and octoploid counts have been reported (Goldblatt, 1981; Moore, 1973).

The phytochemistry of *Lithospermum* is poorly studied, although several species have been surveyed individually for the presence of certain compounds. The data are too fragmentary to be of taxonomic value. The presence of red pigments in the roots of *Lithospermum* is known for many species. In *L. erythrorhizon* Sieb. & Zucc. this dye has been characterized as a mixture of several 1,4-naphthoquinones, including shikonin and its derivatives (Tabata *et al.*). The pigment accumulates in vesicles that originate from spherical swellings of highly elongated, rough endoplasmic reticulum. These vesicles eventually fuse with the plasma membrane to secrete their contents (Tsukuda & Tabata).

Lithospermic acid, which is a biologically inactive phenolic compound in *Lithospermum ruderales* and other members of the genus, produces upon oxidation a polymer that shows antiovarulatory activity and inhibits the effects of exogenous gonadotropin in female rats (Johnson *et al.*).

Seeds of *Lithospermum officinale* are among the richest in the Boraginaceae in linoleic acid and the lowest in linolenic acid (73 and 0.4 percent, respectively). They are also unusual in lacking nonconjugated tetraenoic acids (Kleiman *et al.*).

Johnston's pioneering studies (1952) on pollen morphology of *Lithospermum* paved the way for a better understanding of the relatives of the genus and their boundaries. A few species have been studied palynologically under the scanning electron microscope, and further studies of this kind might reveal more information about the infrageneric structure and phylogeny of the genus.

An anatomical peculiarity in certain species of *Lithospermum* is the development of intercalary cork, a suberized layer of axial parenchyma that originates from the cambium at the end of a growth ring (Carlquist).

Nutlet dispersal of *Lithospermum* is usually limited to short distances estimated to be about one meter from the parent plant. Westelaken & Maun (1985b) suggested that despite the low nutlet production in *L. caroliniense*, the species is fairly successful in sand-dune habitats because of its seed dormancy and its high level of seed survival.

Gabel discovered silicified nutlets of the fossil *Lithospermum dakotense* Gabel from the Late Miocene of South Dakota. Epidermal cells

of the nutlet pericarp showed remarkable similarity to those of extant species. The earlier reports of fossils of *Lithospermum* from North America (e.g., Berry) were shown by Gabel to be based on misidentified material.

Dark purple or red dyes extracted from the roots of many species of *Lithospermum* have been used in Asia and by North American Indians for centuries. The dye, which is insoluble in water but soluble in animal grease, has been used for staining silk and other clothing material and for body decoration. The species most widely used have been *Lithospermum erythrorhizon* in eastern Asia and *L. canescens* and *L. caroliniense* in North America. Roots of the last yield a persistent color that penetrates several adjacent herbarium sheets in a folder. Numerous medicinal properties have been attributed to various species of the genus. These are given in Duke & Ayensu, Moerman, and Perry. The leaves of *L. officinale* are the source of Bohemian or Croatian tea (Uphof). The Owyhee Shoshones of Nevada use *L. ruderale* as a contraceptive. An infusion prepared from the roots of this species and taken by women daily as a drink for six months was said to insure sterility (Train *et al.*). Ingram listed six species, including *L. caroliniense* and *L. canescens*, used as ornamentals.

REFERENCES:

Under family references see AHN & LEE; AL-NOWAIHI *et al.*; BACIU; BAILEY *et al.*; BAILLON; BATE-SMITH; BELL & TAYLOR; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; DE CANDOLLE; CARLQUIST; CHAPMAN; G. C. S. CLARKE; CLEWELL; CORRELL & JOHNSTON; DEAN *et al.*; DUKE & AYENSU; DUNCAN & FOOTE; DUNCAN & KARTESZ; FABRE; FEDOROV *et al.*; FERNALD; GANDERS; GATTINGER; GLEASON; GOLDBLATT (1981, 1984, 1985, 1988); GRAU; HEGI; HIGGINS (1979); HOFFMAN *et al.*; HOMMERSAND; HUNTER; JODIN; JOHNSTON (1924a, 1924b, 1925b, 1927, 1953a, 1953b, 1954a, 1954b); JOHNSTON *et al.*; JONES & COILE; KERNER VON MARILAUN; KLEIMAN *et al.*; KNUTH; LEWIS & ELVIN-LEWIS; LUBBOCK; MACROBERTS; MALECKA; MANSFIELD; MOERMAN; MOHR; R. J. MOORE (1973, 1974, 1977); MUENSCHER; NASH & MORENO; NORTON; ORNDUFF (1968, 1969); PERRY; POLLARD & AMUTI; POPOV (1953); REHDER; RICKETT; RIDLEY; RIEDL (1967); SAHAY; SCHAEFER; SIEBERT; SHARP *et al.*; SMALL (1903, 1933); E. B. SMITH (1978, 1988); STEYERMARK; STREY; SYNGE; TÉTÉNYI; UPHOF; VUILLEUMIER; WARD & FANTZ; WILLAMAN & LI; WILLAMAN & SCHUBERT; WUNDERLIN; and ZEVAN & DE WET.

BAKER, H. G. Heterostyly and homostyly in *Lithospermum canescens* (Boraginaceae). *Rhodora* 63: 229-235. 1961. [Survey of the earlier literature on heterostyly in *Lithospermum*.]

BERRY, E. W. Fossil nutlets of the genus *Lithospermum*. -Proc. U.S. Natl. Mus. 73(13): 1-3. pl. 1. 1928. [*L. fossilum*, a new species with three varieties; study based on misidentified fossils; see GABEL.]

BESSEY, C. E. The supposed dimorphism of *Lithospermum longiflorum* (*L. angustifolium* Michx. of Gray's Synoptical Flora). *Am. Nat.* 14: 417-420. 1880. [Variation in flower size, heterostyly, cleistogamy.]

BRAND, A. Die amerikanischen Arten der Gattung *Lithospermum*. *Repert. Sp. Nov. Reg. Veg.* 28: 10-17. 1930. [Key to 42 species; descriptions of 11 new species.]

- CUSICK, A. W. The Ohio species of puccoon, *Lithospermum canescens* (Michx.) Lehm. and *Lithospermum croceum* Fernald. (Abstr.) Ohio Jour. Sci. **81**: 20. 1981.
- . *Lithospermum* (Boraginaceae) in Ohio, with a new taxonomic rank for *Lithospermum croceum* Fernald. Michigan Bot. **24**: 63–69. 1985. [*L. canescens*, *L. carolinensis* subsp. *croceum* (comb. nov.), *L. latifolium*, *L. officinale*; distinguishing characters, maps.]
- DÍEZ, M. J., B. VALDÉS, & I. FERNÁNDEZ. Pollen morphology of Spanish *Lithospermum* s. l. (Boraginaceae) and its taxonomic significance. Grana **25**: 171–176. 1986. [*L. officinale*; palynology supports the separation of *Lithospermum* from *Neotostoma* and *Lithodora*.]
- DORE, W. G. Discontinuous distribution of the Indian dye-plant, *Lithospermum*, in Canada. (Abstr.) Bot. Soc. Am. Misc. Ser. Publ. **158**: 31, 32. 1980. [*L. carolinense*.]
- EDMONDSON, J. R. *Lithospermum*. In: P. H. DAVIS, ed., Fl. Turkey **6**: 313, 314. 1978. [*L. officinale*, *L. purpurocaeruleum* (= *Buglossoides purpurocaeruleum* (L.) I. M. Johnston).]
- FERNANDES, R. *Lithospermum*. In: T. G. TUTIN et al., eds., Fl. Europaea **3**: 86. 1972. [*L. officinale*.]
- FERNALD, M. L. Critical plants of the upper Great Lakes region of Ontario and Michigan. Rhodora **37**: 324–341. 1935. [*L. croceum*, sp. nov., 329–331, pl. 376.].
- . The validity of *Lithospermum latifolium*. Ibid. **46**: 496, 497. 1944. [Nomenclature.]
- GABEL, M. L. A fossil *Lithospermum* (Boraginaceae) from the Tertiary of South Dakota. Am. Jour. Bot. **74**: 1690–1693. 1987. [*L. dakotense*, sp. nov., from the Late Miocene; scanning electron micrographs of nutlets of fossil and extant *Lithospermum*.]
- GANDERS, F. R. Heterostyly in *Lithospermum cobrense* (Boraginaceae). Am. Jour. Bot. **66**: 746–748. 1979. [Features of heterostyly are same as those of typical distylous plants of other families; comparison with heterostyly of *L. carolinense*.]
- GOVONI, D. N. The taxonomy of the genus *Lithospermum* L. (Boraginaceae) in the western Great Plains. Unpubl. Ph.D. dissertation, Univ. Nebraska. 1973.*
- . Evidence for divergence in *Lithospermum incisum* in the western Great Plains. Taxon **24**: 431–444. 1975. [Numerical analysis of 38 floral and leaf characters using four statistical programs.]
- GRAHAM, R. C. B., & R. L. NOBLE. Comparison of in vitro activity of various species of *Lithospermum* and other plants to inactivate gonadotropin. Endocrinology **56**: 239–247. 1955. [Six species of *Lithospermum* (including *Buglossoides*).]
- HALLECK, D. K., J. H. BOCK, R. R. WEHRMEISTER, & W. H. REID. Pollen studies of florally dimorphic species of *Lithospermum* (Boraginaceae). Jour. Colorado-Wyoming Acad. Sci. **7**: 29. 1975. *
- HEIDE, L., N. NISHIOKA, H. FUKUI, & M. TABATA. Enzymatic regulation of shikonin biosynthesis in *Lithospermum erythrorhizon* cell cultures. Phytochemistry **28**: 1873–1877. 1989.
- HOOKE, W. J. *Lithospermum canescens*. Hoary gromwell. Bot. Mag. **74**: pl. 4389. [2 pp. text.] 1848.
- INGRAM, J. Studies in the cultivated Boraginaceae. 1. *Lithospermum* and related genera. Baileya **6**: 90–100. 1958. [Key to related genera, 92; key to six cultivated species, 99.]
- JOHNSON, G., S. G. SUNDERWIRTH, H. GIBIAN, A. W. COULTER, & F. X. GASSNER. *Lithospermum ruderales*: partial characterization of the principal polyphenol isolated from the roots. Phytochemistry **2**: 145–150. 1962. [Lithospermic acid.]

- JOHNSTON, I. M. Studies in the Boraginaceae, XXIII. A survey of the genus *Lithospermum*. Jour. Arnold Arb. **33**: 299–366. 1952. [Fifty-nine species; taxonomy, palynology; genus includes *Arnebia* and *Macrotomia*.]
- KELLEY, C. J., J. R. MAHAJAN, L. C. BROOKS, L. A. NEUBERT, W. R. BRENNEMAN, & M. CARMACK. Polyphenolic acids of *Lithospermum ruderales* Dougl. ex Lehm. (Boraginaceae). 1. Isolation and structure determination of lithospermic acid. Jour. Organic Chem. **40**: 1804–1815. 1975.
- KERSTER, H. W., & D. A. LEVIN. Neighborhood size in *Lithospermum carolinense*. Genetics **60**: 577–587. 1968. [Models for estimation of gene flow, prevalence of inbreeding despite the development of heterostyly.]
- LEVIN, D. A. The breeding system of *Lithospermum carolinense*: adaptation and counteradaptation. Am. Nat. **102**: 427–441. 1968. [Heterostyly, cleistogamy, pollen flow, self-incompatibility.]
- . Plant density, cleistogamy, and self-fertilization in natural populations of *Lithospermum carolinense*. Am. Jour. Bot. **59**: 71–77. 1972. [Interpopulational variation in self-fertilization and cleistogamy correlated with plant density.]
- LUQUE, T., & B. VALDÉS. Karyological studies on Spanish Boraginaceae: *Lithospermum* L. *sensu lato*. Bot. Jour. Linn. Soc. **88**: 335–350. 1984. [*L. officinale*, *Neatostoma*, *Buglossoides*, *Lithodora*; karyological data suggest three groups that do not correspond to taxonomy.]
- MIZUKAMI, H., M. KONOSHIMA, & M. TABATA. Variation in pigment production in *Lithospermum erythrorhizon* callus cultures. Phytochemistry **17**: 95–97. 1978.
- MUENCHOW, G. E. A temporal heterogeneity hypothesis for the adaptiveness of the chasmogamy/cleistogamy breeding system. (Abstr.) Am. Jour. Bot. **73**(3): 673. 1986. [*L. incisum*.]
- PALACIOS-CHÁVEZ, R., & D. L. QUIROZ-GARCÍA. Catálogo palinológico para la flora de Veracruz. No. 28. Familia Boraginaceae. Género *Lithospermum*. (English summary.) Biotica **10**: 359–362. 1985. [*L. distichum*, pollen tri-, tetra-, or zonocolporate; scanning-electron and light microscopy.]
- RECHINGER, K. H. *Lithospermum Goulandriorum* Rech. f., eine neue, bemerkenswerte Art der griechischen Flora. (English summary.) Bot. Not. **124**: 355–358. 1971. [Subdivisions of *Lithospermum* and related genera discussed.]
- SENN, H. A. The Canadian distribution of *Lithospermum croceum* Fern. Canad. Field-Nat. **52**: 127–128. 1938. [see DORE.]
- SHARP, A. J., & A. BAKER. First and interesting reports of flowering plants in Tennessee. Castanea **29**: 178–185. 1964. [*L. tuberosum* from Knox County, 183.]
- SHAW, R. G. A phytochemical investigation of *Lithospermum ruderales*. Diss. Abstr. **21**: 2494. 1961. [Techniques for separation of gonadotropically active constituents.]
- SMITH, E. F. Trimorphism in *Lithospermum canescens* Lehm. Bot. Gaz. **4**: 168, 169. 1879. [Heterostyly and homostyly in plants from Michigan.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez le *Lithospermum officinale* L. Compt. Rend. Acad. Sci. Paris **235**: 217–219. 1952. [Comparison with embryogeny of *Buglossoides arvensis*.]
- SOURGENS, H., & F. H. KEMPER. Antithyroidal properties of *Lithospermum* and related plants. Acta Endocrinol. Suppl. **96**: 22. 1981.*
- SPENGLER, H. Die verschiedenen Typen im Korollenbau von *Lithospermum*. Österr. Bot. Zeitschr. **68**: 109–123. 2 pls. 1919. [Forty-one species; internal organization of corolla and nutlet morphology, illustrations.]
- STROH, G. Vorläufiges Verzeichnis der altweltlichen Arten der Gattungen *Lithospermum* und *Lithodora*. Beih. Bot. Centralbl. **58B**: 203–212. 1938. [Twenty-five Old World species of *Lithospermum* (including *Buglossoides*) assigned to three sections; comprehensive list of excluded species.]

- SVENSON, H. K. Notes on the Tennessee flora. *Jour. Tenn. Acad. Sci.* **16**: 111-160. 1941. [*L. canescens*, *L. tuberosum*; 154.]
- TABATA, M., H. MIZUKAMI, N. HIRAOKA, & M. KONOSHIMA. Pigment formation in callus cultures of *Lithospermum erythrorhizon*. *Phytochemistry* **13**: 927-932. 1974. [Pigment production controlled by light and auxins.]
- TRAIN, P., J. R. HENRICH, & W. A. ARCHER. Medicinal uses of plants by Indian tribes of Nevada. Contributions toward a flora of Nevada No. 45. 139 pp. Beltsville, Maryland. 1957. (Reprinted, Lawrence, Massachusetts [1982].) [*L. ruderale*, as diuretic and contraceptive, 68.]
- TSUKUDA, M., & M. TABATA. Intracellular localization and secretion of naphthoquinone pigments in cell cultures of *Lithospermum erythrorhizon*. *Pl. Med.* **50**: 338-341. 1984.
- TURNER, B. L. A new species of *Lithospermum* (Boraginaceae) from near El Salto, Durango, Mexico. *Phytologia* **52**: 493, 494. 1983. [*L. Worthingtonii*, sp. nov.]
- WAGNER, H., D. WITTMAN, & W. SCHÄFER. Zur chemischen Struktur der Lithospermsäure aus *Lithospermum officinale* L. *Tetrahedron Lett.* **1975**: 547-550. 1975.
- WARD, D. B. The genus *Anonymos* and its nomenclatural survivors. *Rhodora* **64**: 87-92. 1962. [*L. caroliniense*, 89.]
- WELLER, S. G. Pollen flow and fecundity in populations of *Lithospermum caroliniense*. *Am. Jour. Bot.* **67**: 1334-1341. 1980. [Scanning-electron micrographs of pollen of pin and thrum flowers.]
- . The life history of *Lithospermum caroliniense*, a long-lived herbaceous sand dune species. *Ecol. Monogr.* **55**: 49-67. 1985a. [Pollination, dispersal, dormancy, survivorship.]
- . Establishment of *Lithospermum caroliniense* on sand dunes: the role of nutlet mass. *Ecology* **66**: 1893-1901. 1985b. [Experimental study of the adaptive significance of variation in nutlet mass in relation to survival and emergence.]
- . An experimental approach to the adaptive significance of variation in nutlet mass in *Lithospermum caroliniense* (Boraginaceae). (Abstr.) *Am. Jour. Bot.* **73**(5): 659, 660. 1986.
- . The effect of disturbance scale on sand dune colonization by *Lithospermum caroliniense*. *Ecology* **70**: 1244-1251. 1981. [Experimental study suggests that sand deposition favored the evolution of larger nutlet mass.]
- WESTELAKEN, I. L., & M. A. MAUN. Spatial pattern and seed dispersal of *Lithospermum caroliniense* on Lake Huron sand dunes. *Canad. Jour. Bot.* **63**: 125-132. 1985a. [Ratio of pin to thrum plants, dispersal and predation of nutlets.]
- & ———. Reproductive capacity, germination and survivorship of *Lithospermum caroliniense* on Lake Huron sand dunes. *Oecologia* **66**: 238-245. 1985b. [Reproductive potential greater than actual fruit production; seed dormancy and relatively high rate of seedlings probably enhance the success of *L. caroliniense* on sand dunes.]
- WILBUR, R. L. The identity of Walter's species of *Anonymos*. *Jour. Elisha Mitchell Sci. Soc.* **78**: 125-132. 1962. [*L. caroliniense*, synonymy, 127.]
- WINTERHOFF, H., H.-G. GUMBINGER, & H. SOURGENS. On the antigonadotropic activity of *Lithospermum* and *Lycopus* species and some of their phenolic constituents. *Pl. Med.* **54**: 101-106. 1988. [*Lithospermum officinale*; phenolic profiles, effects of leaf extracts on female rats.]
- WOFFORD, B. E., T. S. PATRICK, L. R. PHILLIPPE, & D. H. WEBB. The vascular flora of Savage Gulf, Tennessee. *Sida* **8**: 135-151. 1979. [*L. tuberosum* in Grundy County, 144.]
- WOOD, C. W. Some American growwells. *Am. Bot.* **40**: 17-19. 1934.
- ZHU, G.-L. A study on the taxonomy and distribution of *Lithospermum* and *Arnebia* in China. (In Chinese; English summary.) *Acta Phytotax. Sinica* **20**: 323-328. 1982. [Five species of *Lithospermum* (including *Buglossoides*), key, map.]

13. *Buglossoides* Moench, Meth. 418. 1794.

Annual [or perennial herbs, rarely shrubs], usually hispidulous or strigillose. Stems erect [to decumbent]. Roots often containing a purplish-red pigment. Leaves entire, obscurely veined. Inflorescences bracteate unilateral cymes, elongating considerably and becoming racemelike after anthesis. Calyx persistent, divided almost to the base into 5 narrow lobes, accrescent in fruit. Corolla funnellform [or hypocrateriform], blue, pink, or creamy white, with 5 imbricate, rounded or truncate lobes; throat lacking faucal appendages but with 5 well-differentiated longitudinal bands of hairs and/or glands extending from the base of the corolla lobe downward to between the tips of anthers; annulus near the base of corolla tube consisting of scalelike lobes or a narrow collar. Stamens included; filaments equal, shorter than anthers; anthers oblong, with a short apical appendage. Style included, about the same height as the anthers, much shorter than calyx; stigmas 2, subterminal. Nutlets typically 4, sometimes fewer by abortion, erect to strongly divergent, ovoid [to pyriform], rounded or angulate, rugose, tuberculate [or smooth]; attachment scar basal or nearly so, conspicuous; gynobase flat or depressed pyramidal. Base chromosome numbers 7, 8, 10. (Including *Aegonychon* S. F. Gray, *Margarospermum* (Reichenb.) Opiz, *Rhytispermum* Link.) TYPE SPECIES: *B. ramosissima* Moench = *B. tenuiflora* (L. f.) I. M. Johnston; see Johnston, 1954a. (Name from *Buglossum* Miller, a generic name now reduced to a section of *Anchusa* L., and *eidos*, appearance, alluding to the superficial resemblance of the two genera. The name *Buglossum* Latin from Greek for ox-tongued, in reference to the broad, rough leaves.)

A genus of about seven species distributed primarily in the European portion of the Mediterranean region and in adjacent southeastern Asia, with a single species, *Buglossoides Zollingeri* (A. DC.) I. M. Johnston, indigenous to China, Korea and Japan. The genus is represented in the southeastern United States by a single cosmopolitan weed.

Buglossoides arvensis (L.) I. M. Johnston (*Lithospermum arvense* L.), corn gromwell, bastard alkanet, $2n = 28, 42$, is a Eurasian annual with oblong-lanceolate leaves; small, funnellform, white to bluish corollas; and dull-brown to grayish, tuberculate, pitted or rough-wrinkled, ovoid nutlets 2–3 mm long. It is a weed of disturbed areas, waste places, roadsides, and fields that has been reported from all of the Southeastern States, where it is most widespread in the Carolinas, Tennessee, and Arkansas.

Buglossoides arvensis is highly variable morphologically, and Fernandes (1972, 1973) divided it into four subspecies, of which three are exclusively Mediterranean. Only subsp. *arvensis* is naturalized in the New World.

The limits of *Buglossoides* are controversial, and some of the species that Johnston (1954a) placed in the genus have recently been retained in *Lithospermum*. In fact, most North American authors have merged

Buglossoides with *Lithospermum*. Between them, Johnston (1954a) and Fernandes (1972) recognized as many as nine species, whereas Miekle assigned only two, or possibly three species to *Buglossoides*. The genus is distinguished from *Lithospermum* in having five vertical, elongated lines of crowded hairs or stipitate glands that extend from the corolla throat to the anthers. In contrast *Lithospermum* has a corolla throat with faucal appendages or groups of stipitate glands that do not form elongated, vertical lines.

Johnston's (1954a) sectional classification of *Buglossoides* has not been followed in the most recent floristic accounts of the family. Section *Margarospermum* (Reichenb.) I. M. Johnston was raised to generic rank (as *Aegonychon*) by Holub and was treated as a section of *Lithospermum* by Popov and Riedl.

Although the flowers of *Buglossoides arvensis* are predominantly autogamous, several pollinators have been reported (Knuth; Svensson & Wigren). The blue- and the white-flowered forms have been recognized as varieties (Hanelt & Schultze-Motel), but such a distinction is unwarranted. Both forms are naturalized in North America. Flowers of the European *B. purpureocaerulea* (L.) I. M. Johnston are said to be protogynous (Knuth). Heterostyly has not been observed in the genus (Johnston, 1954a).

Chromosome numbers have been reported for five species of *Buglossoides*. Both *B. tenuiflora* and *B. arvensis* are tetraploids based on seven, but hexaploids are also known in the latter. *Buglossoides Zollingeri* and *B. purpureocaerulea* are both diploids based on eight, whereas *B. Calabra* (Ten.) I. M. Johnston (southern Italy) is a diploid based on ten. Two pairs of satellite chromosomes have been observed in *B. arvensis* (Fernandes & Leitão) and *B. purpureocaerulea*. The karyotype of the latter and the distribution of telomic bands have been studied by D'Amato.

Pollen grains of *Buglossoides arvensis* are isopolar and predominantly 5-colporate (4- or 6-colporate types are rare), whereas those of *B. purpureocaerulea* are subisopolar and usually 4-colporate. On the basis of pollen and karyotypic differences, Luque & Valdés and Díez *et al.* have argued that the latter species should be assigned to *Aegonychon*, as proposed by Holub. However, the remaining species of *Buglossoides* should be surveyed palynologically and karyotypically before any taxonomic conclusions are reached. Lee & Ahn concluded that pollen data support the placement of sect. *Margarospermum* in *Lithospermum*, rather than retaining it in *Buglossoides*, as Johnston (1954a) did.

Although the fatty-acid composition of seeds of *Buglossoides arvensis* is slightly different from those of *B. purpureocaerulea*, *B. tenuiflora*, and *Lithospermum officinale* (Tétényi; Kleiman *et al.*), the overall profiles apparently are not chemotaxonomically useful.

Three species of *Buglossoides*, *B. Gastonii* (Bentham) I. M. Johnston, *B. purpureocaerulea*, and *B. Zollingeri*, are sometimes grown as

ornamentals (Ingram). The weedy *B. arvensis* is believed to be poisonous to livestock, particularly if ingested in large quantities. Plants of this species grow successfully in grain fields, and their nutlets are often harvested together with the grain. Heavy contamination of feed with nutlets of this species make it unsuitable for long-term feeding.

REFERENCES:

- Under family references see ALTAMURA *et al.*; CLEWELL; G. C. S. CLARKE; DUNCAN & KARTESZ; EVERIST; FERNALD; FERNANDES & LEITÃO; GLEASON; GOLDBLATT (1981, 1984, 1988); GRAU (1968); HOMMERSAND; JOHNSTON (1954a, b); JOHNSTON *et al.*; JONES & COILE; KLEIMAN *et al.*; KNUTH; LEE & AHN; MACROBERTS; R. J. MOORE (1973, 1974, 1977); POPOV (1953); RIEDL (1967); SIEBERT; SMALL (1933); E. B. SMITH (1978, 1988); TÉTÉNYI; TOELKEN; VOYTENKO & OPARINA (1985, 1987); WARD & FANTZ; WOFFORD; and WUNDERLIN.
- AVAKOV, G. S. On the find of *Celtis glabrata* Stev. and *Lithospermum arvense* L. in Lower Quaternary lacustrine deposits of South Georgia. (In Russian.) Dokl. Akad. Nauk SSSR **135**(2): 443, 444. 1960.*
- D'AMATO, G., R. CAPINERI, & P. MARCHI. Heterochromatin localization in *Buglossoides purpureoacerulea* (L.) I. M. Johnston (Boraginaceae): a further case of correspondence between Q⁻ and Feulgen⁺ bands. Caryologia **34**: 395-400. 1981. [Karyotype; patterns of heterochromatin bands following staining with Feulgen, Giemsa, and quinacrine.]
- DÍEZ, M. J., B. VALDÉS, & I. FERNÁNDEZ. Pollen morphology of Spanish *Lithospermum s. l.* (Boraginaceae) and its taxonomic significance. Grana **25**: 171-176. 1986. [*B. arvensis*, *B. purpureoacerulea*; pollen data support the separation of these species to different genera.]
- EDMONDSON, J. R. *Buglossoides*. In: P. H. DAVIS, ed., Fl. Turkey **6**: 315-317. 1978. [*B. arvensis*, *B. incrassata*, *B. tenuiflora*, but *B. purpureoacerulea* treated under *Lithospermum*.]
- FERNANDES, R. *Buglossoides*. In: T. G. TUTIN, *et al.*, eds., Fl. Europaea **3**: 87, 88. 1972. [Seven species recognized.]
- FERNANDES, R. Notes sur le genre *Buglossoides* Moench. (English summary.) Acta Bot. Acad. Sci. Hungar. **19**: 93-101. 1973. [*B. arvensis*, *B. glandulosa*, *B. minima*, *B. tenuiflora*; synonymy, distinguishing characters, distributions; infraspecific taxonomy of *B. arvensis*.]
- GRAU, J. Unterschiede in der Chromosomengestalt bei *Moltkia* und *Lithospermum*. Ber. Deutsch. Bot. Ges. **79**: 182-187. 1966. [*B. purpureoacerulea* (as *Lithospermum*), $2n = 16$.]
- HANELT, P., & J. SCHULTZE-MOTEL. Beobachtungen an einer blaublühenden Sippe von *Lithospermum arvense* L. (English summary.) Kulturpflanze **10**: 122-131. 1962. [Blue-flowered plants recognized as var. *coerulescens* DC.; morphology, ecology, phenology, geography.]
- HOLUB, J. New names in Phanerogamae 2. Folia Geobot. Phytotax. **8**: 155-179. 1973. [*Aegonychon*, a segregate of *Lithospermum*, reinstated; generic limits same as *Buglossoides* sect. *Margarospermum*; 156, 157, 164, 165; see JOHNSTON (1954a).]
- INGRAM, J. Studies in the cultivated Boraginaceae. 1. *Lithospermum* and related genera. Baileya **6**: 90-100. 1958. [*Buglossoides*, 96, 97, 99; key to three cultivated species, illustrations.]
- KOVÁTS, D. Some histological observations on *Lithospermum purpureo-coeruleum* L. seedlings. Ann. Hist.-Nat. Mus. Natl. Hungar. **63**: 99-116. 1971. [Development of xylem in the radicle, hypocotyl, and epicotyl.]

- . Anatomical investigations on the vegetative system of *Lithospermum purpureo-coeruleum*. *Ibid.* **65**: 109–125. 1973. [Anatomy of rhizome, stem, and leaf.]
- . Distribution of internode lengths of two *Lithospermum* species (Boraginaceae). *Ibid.* **75**: 61–70. 1983. [*B. arvensis*, *B. purpureo-coeruleum*.]
- & J. STIEBER. Some observations on the dynamism of structural development in the stem-borne root of *Lithospermum purpureo-coeruleum* L. *Ibid.* **64**: 95–113. 1972.
- LUQUE, T., & B. VALDÉS. Karyological studies on Spanish Boraginaceae: *Lithospermum sensu lato*. *Bot. Jour. Linn. Soc.* **88**: 335–350. 1984. [*B. arvensis*, *B. purpureo-coeruleum*, 337–339.]
- MADRIGAL, R. V., F. E. KNAPP, R. SIGAFUS, & C. R. SMITH, JR. Fractionation of extracts of *Lithospermum arvense* and their activity against mosquito larvae. *Mosquito News* **39**: 536–540. 1979. [Bioassay of extracts, toxicity on *Aedes aegypti*.]
- MALECKA, J. The course of differentiation of the endosperm of *Lithospermum arvense*. *Acta Biol. Cracov. Bot.* **20**: 33–40. *pl.* 3. 1977. [Review of early endosperm differentiation in the Boraginaceae; differences in endosperm development between *B. arvensis* and *Lithospermum officinale*.]
- NAGL, W. Über den unterschiedlichen Formwechsel des Heterochromatins in der mitotischen Prophase von *Lithospermum* und *Lilium*. (English summary.) *Österr. Bot. Zeitschr.* **116**: 295–305. 1969. [*B. purpureo-coeruleum*.]
- PIGNATTI, S. Note critiche sulla Flora D'Italia. VI. Ultimi appunti miscellanei. (English summary.) *Giorn. Bot. Ital.* **113**: 359–368. (1979) 1980. [*B. Gasparrinii*, comb. nov., 360; see FERNANDES (1971).]
- SOSA, A., F. WINTERITZ, R. WYLDE, & A. A. PAVIA. Structure of a cyanoglucoside of *Lithospermum purpureo-coeruleum*. *Phytochemistry* **16**: 707–709. 1977.
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez le *Lithospermum arvense* L. *Compt. Rend. Acad. Sci. Paris* **230**: 2142–2145. 1950. [Cf. SOUÈGES, 1952, under *Lithospermum*.]
- STROH, G. Vorläufiges Verzeichnis der altweltlichen Arten der Gattungen *Lithospermum* und *Lithodora*. *Beih. Bot. Centralbl.* **58B**: 203–212. 1938. [Twenty-five Old World species of *Lithospermum* (including *Buglossoides*) assigned to three sections; comprehensive list of excluded species.]
- SVENSSON, R., & M. WIGREN. Sminkroten historia och biologi i Sverige. (English summary.) *Sv. Bot. Tidskr.* **80**: 107–131. 1986. [*B. arvensis*; distribution in Sweden, germination ecology, flowering, pollination, dispersal.]
- TAYLOR, M., & H. TAYLOR. Plant portrait: *Buglossoides* (*Lithospermum*) *Gastonii*. *Jour. Scot. Rock Gard. Club* **77**: 386, 387. 1986.*
- ZÓLYOMI, B. Synökologische Untersuchung einer Basiphil-Kalziphilen Indikator-Waldpflanze (*Lithospermum purpureo-coeruleum*). *Acta Bot. Hungar.* **9**: 461–472. 1963.*

14. *Onosmodium* Michaux, Fl. Bor. Am. **1**: 132. 1803.

Coarse, erect to ascending, perennial herbs with a well-developed, usually stout rootstock, often densely hispid or strigose, eglandular [or glandular] throughout. Leaves alternate, subsessile [or short petiolate], prominently 3 to 9 veined, the basal ones sometimes forming rosettes. Inflorescences many flowered, bracteate, scorpioid cymes, dense and coiled when young, lax, considerably elongated, and straight in fruit; bracts foliaceous, lanceolate to ovate. Calyx deeply 5-parted, shorter

than corolla, persistent; lobes linear to lanceolate or spatulate, pubescent on the inside and outside. Corolla tubular, yellow, creamy white, or greenish, pubescent outside, glabrous within; throat somewhat expanded, unappendaged; lobes triangular, acute to acuminate, erect, glabrous [or pubescent] on the inside; sinuses between lobes plicate, inflexed, somewhat thickened; annulus glabrous. Stamens 5, included; filaments much shorter than anthers; anthers introrse, lanceolate, sagittate at base, appendaged at apex with prolongation of the connective tissue. Ovary glabrous, deeply 4 lobed, with 1 ovule in each lobe; style gynobasic, filiform, precociously long-exserted, glabrous; stigma slightly 2 lobed. Nutlets 1 or sometimes 2 per fruit, ovoid to subglobose, erect, bony, white or tawny, glossy, smooth or shallowly pitted, [with or] without a constriction above the base; attachment scar flat, bearing remnants of the tubular funicular canal and of the dorsal vascular strand; gynobase flat. Base chromosome numbers 6, 7. (Including *Osmodium* Raf., *Purshia* Sprengel.) LECTOTYPE SPECIES: *O. hispidum* Michx. = *O. virginianum* (L.) A. DC.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. 3: 90. 1913. (Name from likeness to the boraginaceous genus *Onosma*, a name that means *smell of an ass*.) — FALSE GROMWELL, MARBLE-SEED.

A well-defined North American genus of five species, two of which are found in the southeastern United States. Correll & Johnston's estimate of 15 species in the genus is evidently exaggerated. *Onosmodium Helleri* Small is endemic to central Texas and is readily distinguished by its short-petiolate cauline leaves and its fruiting pedicels, which are 5–15 mm long. *Onosmodium unicum* Macbr., restricted to the Mexican states Hidalgo, Nuevo León, and San Luis Potosí, is unusual in the genus for its multicellular, uniseriate, glandular trichomes. Another Mexican endemic, *O. dodrantale* I. M. Johnston (Nuevo León, Tamaulipas), is a very distinct species with small leaves, short stems, few-flowered cymes, and pubescent inner surface of the corolla lobes.

Onosmodium virginianum (L.) A. DC. (*Lithospermum virginianum* L., *O. hispidum* Michx., *Purshia hispida* (Michx.) Lehm., *O. scabrum* Roemer & Schultes; *P. scabra* (Roemer & Schultes) Nutt., *O. virginianum* var. *hirsutum* Mack.), false gromwell, occurs primarily in the eastern United States from eastern New York and eastern Massachusetts south into Virginia and all of the Southeastern States except Tennessee and Arkansas. It is most widespread in the Carolinas, Georgia, and northern and central Florida, where it grows in sandy thickets, open woods, and pinelands, on open sand, and along creek banks. It differs from other species of *Onosmodium* in its light-yellow to orange flowers and narrowly lanceolate, acuminate corolla lobes two to three times as long as broad.

Onosmodium molle Michx. (*Lithospermum molle* (Michx.) Muhl., *Purshia mollis* (Michx.) Lehm.), false gromwell, is the most variable species in the genus. Five of the principal variants were recognized by Britton & Brown, Correll & Johnston, Fernald, Gleason, Johnston

(1924, 1954), and Johnston *et al.* as distinct species, by Cochrane as subspecies, and by Cronquist as varieties. In my opinion these variants are weakly defined and perhaps are better treated as subspecies, rather than species. Four of the five subspecies of *O. molle* grow in the Southeast; subsp. *bejariense* (A. DC.) Cochrane is restricted to central Texas.

Onosmodium molle subsp. *molle* is distributed primarily in the Nashville Basin, Tennessee (Carroll, Davidson, Giles, Maury, Rutherford, Trousdale, and Wilson counties), and is uncommon in Alabama (Franklin County), Kentucky (Logan County), and Illinois (Jackson County). A record from Durham County, North Carolina (Hommersand) was apparently based on plants of *O. virginianum* (Baskin, Baskin, & Medley). Subspecies *molle* grows primarily in shallow soil overlying limestone bedrock, particularly in cedar glades, pastures, and old fields, as well as along powerline rights-of-way and roadsides.

Onosmodium molle subsp. *occidentale* (Mack.) Cochrane (*O. occidentale* Mack., *O. molle* var. *occidentale* (Mack.) I. M. Johnston), $2n = 28$, is the most widely distributed member of the genus. Its range extends from southeastern Alberta south through central Montana, eastern Wyoming, central Colorado, into northeastern New Mexico, eastward into northeastern Texas, Oklahoma, into Missouri, western Illinois, Minnesota, and Manitoba. Das did not record it from any of the Southeastern States, but Baskin, Baskin & DeSelm reported it from Alabama (Colbert and Sumter counties), Georgia (Catoosa), Mississippi (Clay and Yazoo), and Tennessee (Decatur, Knox, and Meigs), as well as from Kentucky and Virginia, and Smith (1988) mapped it from five counties (Hempstead, Little River, Newton, Sevier, and Washington) in Arkansas. Subspecies *occidentale* is distinguished from subsp. *molle* by its longer corollas (11–15 mm), larger nutlets (3.8–5 mm) that are not constricted at the base, and leaves that are not grayish. In contrast subsp. *molle* has corollas 7.5–10 mm long, nutlets 2.7–3.5 mm long and slightly constricted at the base, and grayish-pubescent leaves.

A third subspecies, *Onosmodium molle* subsp. *subsetosum* (Mack. & Bush) Cochrane (*O. subsetosum* Mack. & Bush, *O. molle* var. *subsetosum* (Mack. & Bush) Cronq.), is widely distributed in northern and central Arkansas, eastern Oklahoma, and central and southern Missouri. It has been reported recently from Franklin and Rutherford counties, Tennessee (Patrick *et al.*). It is distinguished from the other subspecies of *O. molle* in having stems that are glabrous and shining below and strigose above.

Onosmodium molle subsp. *hispidissimum* (Mack.) Boivin (*O. hispidissimum* Mack., *O. molle* var. *hispidissimum* (Mack.) Cronq., *O. hispidissimum* var. *macrosperrum* Mack.), $2n = 24$, is distributed from Minnesota east into central New York, south into the Virginias, and west into Missouri. The subspecies has been reported from Arkansas (Smith, 1988), Louisiana (Fernald; Mackenzie; MacRoberts), Tennessee (Fernald; Kral; Mackenzie; Patrick *et al.*; Wofford) and North Carolina (Fernald; Mackenzie; Rickett; Small, 1933), but I have not

seen any material from these states. Fruiting specimens of subsp. *hispidissimum* are readily distinguished from those of other taxa in having nutlets strongly constricted at the base. Subspecies *hispidissimum*, *molle*, and *bejariense* all have large, spreading trichomes mixed with smaller, appressed ones on the upper leaf surfaces. Cochrane's new combination (as subsp. *hispidissimum*) is antedated by Boivin's by four years.

Except for the *Onosmodium molle* complex, other species of the genus are well marked, but members of the *O. molle* complex are not so well defined. Several authors (e.g., Cochrane, Cronquist, Das) have indicated that the various extremes of *O. molle* intergrade, and Das cited intermediates between subsp. *occidentale* and all the other taxa (as varieties) of *O. molle*, as well as between subsp. *hispidissimum* and both subsp. *bejariense* and subsp. *molle*. Das attributed the occurrence of intermediates between these taxa to introgressive hybridization. In contrast Kral and Patrick *et al.* have noted that these subspecies (as species) grow sympatrically in Tennessee and apparently do not produce intermediates. Evidently, the *O. molle* complex is in need of comprehensive experimental and field studies. Although Johnston (1954) recognized the various morphological extremes as species, he was the first to question the validity of their rank and to indicate that they intergrade and lack sharp definition.

Onosmodium is apparently related to *Lasiarrhenum* I. M. Johnston and *Macromeria* D. Don and is more closely related to *Lithospermum* than to any other genus of the Lithospermeae (Johnston, 1954). The genus is readily distinguished by its long-exserted styles and its tubular corollas, which have erect, triangular lobes, plicate, inflexed, thickened sinuses, and lack either faucal appendages or trichomes at the throat. Macbride expanded the limits of the genus to include species now assigned to *Macromeria* and *Psilolaemus* I. M. Johnston.

Hardly anything is recorded about the reproductive biology of *Onosmodium*. Johnston (1954) emphasized that flowers of all species are precociously sexual. A young flower has its corolla open, its anthers mature, and its style exserted long before the corolla attains its full length. The protrusion of the style from the flower bud takes place at a stage when the corolla is shorter than the calyx. Therefore, the flowers are so strongly protogynous that, according to Johnston (1954), self-pollination (p. 22) "is practically impossible." Sexually precocious flowers in the Boraginaceae are also known in the European monotypic *Halacsya* Dörfler, a remotely related member of the Lithospermeae.

Chromosome numbers are known for *Onosmodium molle* subsp. *hispidissimum*, $2n = 24$ (Löve & Löve), and subsp. *occidentale*, $2n = 28$ (Smith, 1965). Additional counts, particularly in the *O. molle* complex, are needed before anything can be said about chromosomal evolution within the genus.

The fatty acids of *Onosmodium molle* were studied by Kleiman *et al.*, who found that the seeds contain comparable amounts of linolenic (24 percent), 6,9,12-octadecatrienoic (20 percent), linoleic (19 percent),

and oleic (19 percent) acids. They also contain smaller amounts of palmitic, tetraenoic, and stearic acids (eight, six, and three percent, respectively). Gross & Dorrell found very similar concentrations of these acids in subsp. *occidentale* and suggested that plants of the taxon are potentially useful as a source of industrial oil because of their very high ratio of unsaturated to saturated fatty acids.

The genus apparently has little, if any, economic value at present. Moerman stated that the Cheyenne Indians used the smashed leaves and stems of subsp. *occidentale* to rub numb skin and to treat lumbago, and that the Hopi Indians use plants of the genus in witchcraft medicine and as an anticonvulsive.

REFERENCES:

- Under family references see BAILLON; BENTHAM & HOOKER; BRITTON & BROWN; DE CANDOLLE; CHAPMAN; CLEWELL; CORRELL & JOHNSTON; CRONQUIST (1959); DUNCAN & KARTESZ; FERNALD; GATTINGER; GLEASON; HIGGINS (1979); HOMMER-SAND; JOHNSTON (1924a, 1954b); JOHNSTON *et al.*; JONES & COILE; KLEIMAN *et al.*; LAKELA *et al.*; MACROBERTS; MOERMAN; MOHR; PARK; POLLARD & AMUTI; RICKETT; SAHAY; SEIBERT; SHARP *et al.*; SMALL (1903, 1933); E. B. SMITH (1978, 1988); STEYERMARK; WARD & FANTZ; WOFFORD; and WUNDERLIN.
- BASKIN, J. M., C. C. BASKIN, & H. R. DESELM. *Onosmodium molle* subsp. *occidentale* in Tennessee and the Southeast. *Castanea* 51: 152, 153. 1986. [County records from Alabama, Georgia, Mississippi, and Tennessee.]
- , ——— & M. E. MEDLEY. The historical geographic distribution of *Onosmodium molle* Michx. subsp. *molle* (Boraginaceae). *Bull. Torrey Bot. Club* 110: 73–76. 1983. [Distribution in Alabama, Kentucky, Illinois, and Tennessee; evaluation of records from other states; map.]
- BOIVIN, B. Flora of the Prairie Provinces. Part III—Connatae. *Phytologia* 22: 315–398. 1972. [*Onosmodium*; two taxa recognized in Canada, 372.]
- COCHRANE, T. S. Taxonomic status of the *Onosmodium molle* complex (Boraginaceae) in Wisconsin. *Michigan Bot.* 15: 103–110. 1976. [*O. molle* divided into four subspecies; morphology, distribution, key, new combinations.]
- DAS, T. L. A taxonomic revision of the genus *Onosmodium*. ii + 80 pp. Unpubl. M.S. thesis. Kansas State University. Manhattan, Kansas. 1965. [Five species recognized, and five varieties in *O. molle*; key, descriptions, distribution, illustrations, map.]
- GOODMAN, G. J. Notes on Oklahoma plants. *Proc. Okla. Acad. Sci.* 32: 39, 40. 1952. [*Onosmodium subetosum* Mack. & Bush, 39.]
- GROSS, A. T. H., & D. G. DORRELL. Seed and oil characteristics of *Onosmodium occidentale*. *Canad. Jour. Pl. Sci.* 56: 659–664. 1976. [Fatty-acid composition, variation of oil content within plants, potential industrial value.]
- JOHNSTON, I. M. Studies in the Boraginaceae, XII. *Jour. Arnold Arb.* 18: 1–25. 1937. [*O. dodrantale*, sp. nov., 22.]
- . Studies in the Boraginaceae, XXVI. Further revaluations of the genera of the Lithospermeae. *Jour. Arnold Arb.* 35: 1–81. 1954. [*Onosmodium*, 18–24.]
- KRAL, R. A report on some rare, threatened or endangered forest-related vascular plants of the South. U.S. Dep. Agr. Forest Serv. South. Reg. Tech. Publ. R8-TP 2. Vol. 2. iv + 719–1305 pp. 1983. [*O. molle*, description, distribution, habitats, map, 924–928.]
- LELONG, M. G. Annotated list of vascular plants in Mobile, Alabama. *Sida* 7: 118–146. 1977. [*O. virginianum*, 140.]

- LÖVE, Á., & D. LÖVE. In: IOPB chromosome number reports LXXV. Taxon **31**: 342–368. 1982. [*O. molle* subsp. *hispidissimum*, 353, $2n = 24$.]
- MACBRIDE, J. F. Further notes on the Boraginaceae. Contr. Gray Herb. **49**: 16–22. 1917. [*Onosmodium*, 19–22; generic limits, five species of *Macromeria* and *Lithospermum* transferred to *Onosmodium*; *O. unicum*, sp. nov.; see JOHNSTON, 1954.]
- MACKENZIE, K. K. *Onosmodium*. Bull. Torrey Bot. Club **32**: 495–506. 1905. [Seven species and three varieties recognized, key, new taxa.]
- PATRICK, T. S., B. E. WOFFORD, & D. H. WEBB. State records and other recent noteworthy collections of Tennessee plants. IV. Castanea **48**: 109–116. 1983. [*O. subsetosum* in Franklin and Rutherford counties, 113.]
- ROGERS, K. E. Vascular flora of Ragland Hills area, Forrest and Perry counties, Mississippi. Sida **7**: 51–79. 1977. [*O. virginianum*, infrequent in open pinelands, 55.]
- SMITH, E. B. Chromosome numbers of Kansas flowering plants. II. Trans. Kans. Acad. Sci. **68**: 463, 464. 1965. [*O. occidentale*, $2n = 28$.]
- VAN HORN, G. S. Additions to the cedar glade flora of Northwest Georgia. Castanea **45**: 134–137. 1980. [*O. molle* var. *occidentale* in Catoosa County.]

15. *Echium* Linnaeus, Sp. Pl. 1: 139. 1753; Gen. Pl. ed. 5. 68. 1754.

Biennial [annual, or perennial] herbs [monocarpic shrubs, large shrubs or small trees], hispid or strigose, usually with tubercle-based setae mixed with shorter, spreading or appressed trichomes. Basal leaves (in herbaceous plants) petiolate, rosulate, entire; cauline leaves numerous, sessile [sometimes amplexicaul]. Inflorescences densely flowered, bracteate helicoid cymes grouped in many-branched thyrses or panicles, elongated considerably in fruit; flowers sometimes resupinate, somewhat bilabiate. Calyx deeply 5 lobed, usually accrescent, the two adaxial lobes usually smallest. Corolla bright blue (pink in bud) [purple, or pink], rarely white [red, or yellowish], zygomorphic, funnellform [trumpet shaped, or tubular], pubescent [or rarely glabrous] on the outside; limb markedly oblique, the lobes imbricate, ascending, equal [or unequal]; throat open, without faucal appendages; tube tapering to base, the annulus within nearly basal, pubescent [or glabrous], represented by 5–10 lobes [rarely reduced to a narrow ring]. Stamens 5, variously exserted [or all included]; filaments slender, unequal [or equal] in length, inserted deeply on the corolla tube at various levels [rarely at the same level], glabrous [or rarely pilose]; anthers oblong, cordate at base. Ovary deeply 4 lobed, 4 ovulate; style exserted, pubescent, forked [or not] near the tip; stigmas 2, distinct, capitate. Nutlets 4 (or fewer by abortion), ovoid [lance-ovoid, or globose], erect, straight [or incurved], scrobiculate-reticulate [tuberculate, rugose or smooth], strongly keeled adaxially (ventrally); attachment scar basal, broad; gynobase flat [or occasionally broadly pyramidal]. Base chromosome numbers 5, 7, 8, 12. (Including *Argyrexias* Raf., *Isoplesion* Raf., *Larephes* Raf., *Megacaryon* Boiss.) LECTOTYPE SPECIES: *E. italicum* L.; see

Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. **3**: 93. 1913.¹² (Name from Greek *echis*, viper, in reference to the superficial resemblance of the nutlet to a viper's head. Consequently, and because of the belief in the Doctrine of Signatures, the plant was used in ancient times to cure snake bites.)—VIPER'S BUGLOSS.

A taxonomically difficult genus of about 60 species distributed primarily in the Mediterranean region,¹³ but with the center of greatest morphological diversity in Macaronesia, 22 species being indigenous to the Canary Islands, three to the Cape Verde Islands, and two to Madeira (Bramwell, 1972b). There are about 26 species native to northwestern Africa, with the richest concentration in Morocco, and about 15 to the Iberian Peninsula (Gibbs, 1971). At least five species are weedy and widely distributed in Eurasia and North Africa. Two of these are naturalized in the New World, and one is represented in the southeastern United States.

Echium vulgare L. (see Klotz 1962b for 21 synonyms), blue devil, blue weed, viper's bugloss, $2n = 16, 32$, a European weed widely distributed in the United States and Canada, has been reported from North and South Carolina, Georgia, Tennessee, Arkansas, and Louisiana. Dean *et al.* reported the species from Alabama: Johnston (1924a), Duncan & Kartesz, and Small (1933) indicated that the species grows in Georgia, but Jones & Coile did not include it in their distribution maps. Johnston (1924a) also listed it for Louisiana, but MacRoberts considered its presence there questionable.

Plants of *Echium vulgare* with sparse, ridged setae originating from white tubercles and with long cymes in pyramidal panicles have been recognized by some authors as *E. pustulatum* Sibth. & Sm. and by others (e.g., Fernald; Gleason; Johnston, 1924a) as *E. vulgare* var.

¹²Johnston (1953) followed Hitchcock & Green's choice of *Echium vulgare* L. as the lectotype, but Britton & Brown, who were the first to lectotypify the genus, selected *E. italicum*, the second of six species recognized by Linnaeus (Sp. Pl. **1**: 139, 140. 1753). The first Linnaean species, *E. fruticosum* L., was transferred by Buek to *Lobostemon* Lehm., a genus that did not receive full recognition until Levyns' revision in 1934. Hitchcock & Green (p. 128) argued that their selection as a lectotype of *E. vulgare*, the third of the Linnaean species, was based on the fact that it is "The best known of the four species retained in the genus. The only Swedish species. Two species are now excluded from the genus, *E. fruticosum* and *E. orientale*." These authors probably overlooked Johnston's (1924b) union of *Lobostemon* with the earlier published *Echium* and his transfer of all species of the former to the latter. Although Johnston did not mention *E. fruticosum*, it is quite evident that his circumscription of *Echium* includes this species. Furthermore, *E. orientale* is now retained in the genus (Edmondson; Johnston, 1953). Britton & Brown's selection of *E. italicum* as the lectotype is perfectly valid and is more solid evidence that these authors did not always follow a mechanical procedure in the typification of genera. In a later publication, Johnston (Johnston *et al.*) changed his mind and followed Britton & Brown's choice of *E. italicum* as the generic lectotype. Index Nominum Genericorum (Regnum Veg. **100**: 596. 1979) lists this species as the lectotype, and Hitchcock and Green's lectotypification has been widely ignored.

¹³The number above does not include "species" described by Sennen, viz., 21 for Morocco and four for Spain.

pustulatum (Sibth. & Sm.) Coiney. As indicated by Gibbs (1972) and Pusateri & Blackwell, the two intergrade. In fact the distinction between these "varieties" is often artificial among the North American material, and therefore any formal recognition of the morphological extremes of *E. vulgare* is not recommended.

All except one of the eight sections recognized in *Echium* by Bramwell (1972b, 1975) are endemic to Macaronesia. Section ECHIUM (annual or biennial herbs, basal rosettes present or absent, some or all stamens included within the corolla) includes *E. vulgare*, as well as two Canarian annuals and all the species that occur outside Macaronesia. The other sections are not dealt with here.

The generic limits of *Echium* were expanded by Johnston (1924b) to include the South African genus *Lobostemon* Lehm., members of which have undivided styles and hairy scales at the base of the staminal filaments, whereas those of the former have 2-lobed or furcate styles and no scales at the base of the filaments. Johnston argued (p. 51) that he had "searched in vain for characters which would distinguish generically the South African species [*Lobostemon*] from those north of the equator." However, in his comprehensive accounts of the Lithospermeae, he (Johnston, 1953, 1954b) recognized the two genera as distinct. *Echium* is readily distinguished from all other genera of the Boraginaceae in the United States by its zygomorphic, funnelform corollas without faucal appendages, exerted stamens, pubescent styles, and adaxially keeled nutlets that have a large basal attachment scar.

The diversity in habit of the Canarian species of *Echium* is not paralleled by that of any other genus in the Boraginaceae. *Echium triste* includes infraspecific taxa that are annual, biennial, or perennial herbs. A few (e.g., *E. simplex* DC. and *E. Pininana* Webb & Berth.) are monocarpic, unbranched subshrubs that produce inflorescences as high as 2 and 3.5 m, respectively, while many are large shrubs with thick stems, shaggy bark, and candelabra-like branching (Bramwell, 1972b; Carlquist, 1974). On the basis of wood anatomy, Carlquist (1970) emphasized that evolution in the Macaronesian species has been toward increased woodiness, and that the shrubby insular species are secondarily woody and derived from continental herbaceous species. In this he agreed with Johnston (1953), who reached a similar conclusion on the basis of overall morphology. However, this view has been seriously challenged by Bramwell (1973), who proposed that the woody Macaronesian species are less specialized and showed that they are self-incompatible outbreeders with a relatively high percentage of gynodioecism. He suggested that the shortening of life duration and reduction of woody habit was accompanied by a reduction in base chromosome number and an increase in ploidy level. The predominance of self-incompatibility and diploidy in the Macaronesian species were considered by Bramwell to be reliable measures of primitiveness.

Aldridge used the length to width ratios of vessels and libriform fibers, as well as various aspects of the rays and trichomes, to study

the phylogenetic relationships among 17 Macaronesian species of *Echium*. She concluded that Carlquist's (1970) sampling techniques were unsatisfactory and that the genus is primitively woody in Macaronesia.

Protandry and gynodioecism are apparently very common in *Echium* (Johnston, 1953), whereas protogyny and gynomonoeism are relatively rare. Species with homogamous flowers are common. Knuth gave a detailed account of the pollination biology of *E. vulgare* in Europe and listed as pollinators numerous species of insects, especially bees, butterflies, hoverflies, and moths. The flowers of *E. vulgare* are typically protandrous: during anther dehiscence the stigmatic lobes are very closely appressed to each other, and it is only after pollen is released that they diverge and become receptive. The flowers remain open for three to four days (Corbet). Vereshchagina (1971, 1976) described gynodioecism in *E. vulgare* and Schulz (in Knuth) showed that the carpellate flowers have smaller corollas and shorter styles than the hermaphroditic ones and that they produce aborted pollen. The number of carpellate plants within a given population can be quite variable; sometimes they constitute as much as 75 percent of the population (Schulz; see Knuth). Protandry has also been observed in *E. plantagineum*, but because of the rapid floral development, its effectiveness in promoting outcrossing is highly reduced (Burdon *et al.*, 1988).

The Canarian *Echium Wildpretii* Pearson ex J. D. Hooker has protogynous red flowers that are pollinated by bees and birds. The apices of the corolla lobes reflect ultraviolet light. During the first of three days in which the flowers remain open, pollen is shed from the anthers; autogamy in the species takes place.

Bramwell (1972a) estimated pollen sterility in populations of six Macaronesian species of *Echium* to be as high as 17 to 30 percent. He reported self-incompatibility and gynodioecism in several species and indicated that self-pollination results in zero to eleven percent seed set, whereas cross-pollinated plants produced 60 to 90 percent seed set.

Chromosome numbers have been determined for 40 species of *Echium* (ca. 67 percent of total). The genus is almost uniformly based on eight, and only three species, *E. asperrimum* Lam. ($2n = 14, 28$), *E. Boissieri* Steudel ($2n = 10$), and *E. russicum* J. F. Gmelin ($2n = 12, 24$) deviate from that. Six species have both diploid and tetraploid populations, and only *E. gaditanum* Boiss., *E. rosulatum* Lange, and *E. tuberculatum* Hoffmans., are tetraploids based on $x = 8$ (Fritsch; Luque).

Bramwell (1973) concluded that the primitive base chromosome number for *Echium* is eight and observed that most of the Macaronesian species have uniform metacentric chromosomes with a pair of satellites. Other base numbers (7, 6, 5) were derived from $x = 8$ by centromeric loss.

Natural interspecific hybridization has been reported by Bramwell (1973) between the Canarian *Echium brevirame* Sprague & Hutchinson (sect. *Gigantea* (Christ ex Sprague & Hutchinson) Bramwell) and *E. Webbii* Coincy (sect. *Virescentia* (Christ ex Sprague & Hutchinson)

Bramwell). The hybrid, *E. × Bond-spraguei* Sprague & Hutchinson, recombines with both parents. Other intersectional hybrids between *E. Decaisnei* Webb & Bert. (sect. *Decaisnea* Bramwell) and each of *E. strictum* L. f. (sect. *Stricta* (Christ ex Sprague & Hutchinson) Bramwell) and *E. virescens* DC. (sect. *Virescentia*) have been named *E. × Lemsii* Kunkel and *E. × Lidii* Kunkel, respectively (Kunkel; Kunkel & Kunkel).

The fatty acid composition of *Echium italicum*, *E. plantagineum*, and *E. vulgare* has been surveyed (Kleiman *et al.*; Tétényi). The last species has higher concentrations (ca. 33 percent) of oleic acid and smaller amounts (ca. 17 percent) of linolenic acid than the other species.

On the basis of trichome morphology, Lems & Holzapfel (1968a) concluded that the monocarpic habit of *Echium Pininana*, *E. simplex*, and *E. Wildpretii* evolved independently from different shrubby ancestors that had a candelabra-like habit. Bramwell (1973) found, however, that these three species contain a unique dimethylated flavone not found elsewhere in *Echium*. He concluded that the three species form a monophyletic group supported by similarities in habit and floral morphology.

Esau & Thorsch studied 15 species of *Echium* and found that they all contain phloem crystalloids that are composed of tightly packed narrow tubules. They are developed in nuclei of sieve-tube elements during the early stages of cellular differentiation from the procambial derivatives, and when the nucleus disintegrates the crystalloids are released into the lumen of the sieve-tube element.

Several species of *Echium* are popular ornamentals, and others (e.g., *E. plantagineum*) are noxious weeds in Australia. Quinones extracted from tissue cultures of this species (as *E. Lycopsis*) were shown to inhibit the growth of gram-positive bacteria. A few medicinal attributes of *E. vulgare* are given by Moerman and Uphof. The stiff, bristly hairs of several species are known to cause contact dermatitis with itching and inflammation (Mitchell & Rook; Steyermark). Sheep feeding on plants of *E. plantagineum* were found to develop symptoms associated with liver toxicity (Everist; Kingsbury).

REFERENCES:

- Under family references see AL-NOWAIHI *et al.*; ALTAMURA *et al.*; BACIU; BAILEY *et al.*; BAILLON; BATE-SMITH; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BREEMAN; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; H. M. BURKILL; DE CANDOLLE; G. C. S. CLARKE; DEAN *et al.*; DíEZ (1984); DI FULVIO (1965b); DUNCAN & KARTESZ; EVERIST; FABRE; FEDOREEV & KRIVOSHCHEKOVA; FERNALD; FERNANDES & LEITÃO; GATTINGER; GLEASON; GOLDBLATT (1981, 1984, 1985, 1988); HEGI; HOFFMAN *et al.*; HOMMERSAND; HUNTER; JODIN; JOHNSTON (1924a, b, 1927, 1954b); JOHNSTON *et al.*; JONES & COILE; KERNER VON MARILAUN; KINGSBURY; KLEIMAN *et al.*; KNUTH; LEVYNS; LEWIS & ELVIN-LEWIS; LOEW; LUBBOCK; LUQUE (1980); MALECKA; MARTICORENA; R. B. MILLER; MITCHELL & ROOK; MOERMAN; R. J. MOORE (1973, 1974, 1977); MUENSCHER; ORNDUFF (1967, 1968, 1969); PARK; POLLARD & AMUTI; POPOV (1953); RICKETT; RIDLEY; RIEDL (1967); SAHAY; SCOTT & KENNEALLY; SEIBERT; SHARP *et al.*; SMALL (1903, 1933); E. B.

SMITH (1978, 1988); SMITH & CULVENOR; STEYERMARK; STREY; SYNGE; TÉTÉNYI; THORSCH & ESAU; TOELKEN; UPHOF; VOYTENKO & OPARINA (1985); WILLAMAN & LI; WILLAMAN & SCHUBERT; and WOFFORD.

ALDRIDGE, A. E. Anatomy and evolution in Macaronesian *Echium* (Boraginaceae). Pl. Syst. Evol. **138**: 9–22. 1981. [Wood anatomy of 17 species, evolutionary trends and phylogenetic relationships.]

ANDERSON, A. W. The genus *Echium*. Gard. Chron. **121**: 72, 73. 1947. [Notes on several cultivated species.]

BAAS, J. Ein bedeutsamer prähistorischer Pflanzenfund der Gattung *Echium* Linné aus dem Libanon. Nat. Mus. **107**: 78–82. 1977.*

BALLARD, L. A. T., & A. E. G. LIPP. Differential specificity exhibited by two germination inhibitors present in *Echium plantagineum* L. Austral. Jour. Biol. Sci. **12**: 343–347. 1959. [Effects of water and alcohol extracts from *E. plantagineum* on seed germination of this and several other species.]

BOIS, D. Les *Echium* arborescents. Bull. Soc. Natl. Acclimation France **59**: 716–720. 1912. [Notes on the monocarpic species.]

BRAMWELL, D. Some notes on *Echium* (Boraginaceae) from Lanzarote and Fuerteventura. Cuad. Bot. Canar. **12**: 3–7. 1971. [Taxonomic and nomenclatural notes; new combinations in the ranks of subspecies, varietas, and forma.]

———. Breeding systems in Canary Island *Echium* species. Internatl. Organ. Pl. Biosyst. Newsl. **6**: 2–9. 1972a. [Protandry, gynodioecism, and self-incompatibility in many species.]

———. A revision of the genus *Echium* in Macaronesia. Lagascalia **2**: 37–115. 1972b. [Twenty-eight species in eight sections; habit and growth forms, scanning-electron microscopy of trichomes, floral morphology, relationships within sections, distributions, descriptions, key, maps; the basic treatment. Macaronesia = the eastern Atlantic islands: the Azores, Madeira, the Canary and Cape Verde Islands.]

———. Studies in the genus *Echium* from Macaronesia. Monogr. Biol. Canar. **4**: 71–82. 1973. [Flavonoid chemistry of 16 species, cytology, evolutionary trends, interspecific hybridization, scatter diagram.]

———. Some morphological aspects of the adaptive radiation of Canary Islands *Echium* species. Anal. Inst. Bot. Cavanilles **32**: 241–254. 1975. [Sectional classification; evolution of habit, leaf types, physiological diversification.]

BREEMEN, A. M. M. VAN. Comparative germination ecology of three short-lived monocarpic Boraginaceae. Acta Bot. Neerl. **33**: 283–305. 1984. [*E. vulgare*; effects of light, moisture, and temperature on seed germination.]

——— & B. H. VAN LEEUWEN. The seed bank of three short-lived monocarpic species, *Cirsium vulgare* (Compositae), *Echium vulgare* and *Cynoglossum officinale* (Boraginaceae). (Abstr.) Ibid. **32**: 245, 246. 1983. [Seed survival within 14 populations of *E. vulgare* during four years.]

BROWN, A. H. D., & J. J. BURDON. Multilocus diversity in an outbreeding weed, *Echium plantagineum* L. Austral. Jour. Biol. Sci. **36**: 503–509. 1983. [Genetic structure of a population at 23 isozyme loci; heterozygosity and locus polymorphism; average alleles per locus is three.]

BRUNO, F. An exceptional case of fasciation in *Echium plantagineum*. (In Italian; English summary.) Ann. Bot. Roma **28**: 465–468. pls. 34, 35. 1965.

BUEK, H. W. *Echia capensis*. Linnaea **11**: 129–149. 1837. [Several species previously assigned to *Echium* transferred to *Lobostemon*; new taxa.]

BURDON, J. J., & A. H. D. BROWN. Population genetics of *Echium plantagineum* L.—target weed for biological control. Austral. Jour. Biol. Sci. **39**: 369–378. 1986. [Genetic variability of ten populations at 16 isozyme loci; estimation of heterozygosity.]

- , D. R. MARSHALL, & A. H. D. BROWN. Demographic and genetic changes in populations of *Echium plantagineum*. *Jour. Ecol.* **71**: 667–679. 1983. [Genetic changes within populations, seedling mortality, competition between white- and blue-flowered forms; electrophoresis of four enzymes.]
- , A. M. JAROSZ, & A. H. D. BROWN. Temporal patterns of reproduction and outcrossing in weedy populations of *Echium plantagineum*. *Biol. Jour. Linn. Soc.* **34**: 81–92. 1988. [Estimation of outcrossing, seed output, temporal variation in flowering and outcrossing rates.]
- CARLQUIST, S. Wood anatomy of *Echium* (Boraginaceae). *Aliso* **7**: 183–199. 1970. [Thirteen species; dimensions of vessel elements, fibers, and rays; ecological and phylogenetic implications.]
- . *Island biology*. ix + 660 pp. New York and London. 1974. [*Echium*, 182–191; 16 photographs showing habit of various species.]
- COINCY, A. DE. Revision des espèces critiques du genre *Echium*. *Jour. Bot. Morot* **14**: 297–304, 322–330. 1900; **15**: 311–328. 1901; **16**: 66–68, 107–112. 1902. [Detailed descriptions, synonymies, and ranges of 20 species.]
- . Énumération des *Echium* de la flore Atlantique. *Ibid.* **16**: 213–220, 226–233, 257–266. 1902. [Sectional classification, taxonomic notes and distributions of 21 species, new taxa.]
- . Les *Echium* de la section des *Pachylepis* sect. nov. *Bull. Herb. Boiss.* II. **3**: 261–277, 488–499. 1903. [Treatment of 19 species.]
- CORBET, S. A. Bee visits and the nectar of *Echium vulgare* L. and *Sinapis alba* L. *Ecol. Entomol.* **3**: 25–37. 1978. [Temporal and ecological factors influencing concentrations and amounts of nectar, honeybee visits, anthesis.]
- . Bees and the nectar of *Echium vulgare*. Pp. 21–30 in A. J. RICHARDS, ed., *The pollination of flowers by insects*. London. 1979. [Temporal fluctuation in volume and concentration of nectar.]
- & E. S. DELFOSSE. Honeybees and the nectar of *Echium plantagineum* L. in southeastern Australia. *Austral. Jour. Ecol.* **9**: 125–139. 1984. [Effects of temperature, humidity, temporal factors, and flower density on nectar production; estimation of nectar concentration and production per flower; bee activities in flower visitations.]
- CULVENOR, C. C. J. The alkaloids of *Echium plantagineum* L. *Austral. Jour. Chem.* **9**: 512–520. 1956. [Isolation and characterization of the new pyrrolizidine alkaloids echiumine and echimidine.]
- , J. A. EDGAR, & L. W. SMITH. Pyrrolizidine alkaloids in honey from *Echium plantagineum*. *Jour. Agr. Food Chem.* **29**: 958–960. 1981. [Honey produced from stands of this species contained eight pyrrolizidine alkaloids totalling about 0.27 to 0.95 ppm; echimidine the main alkaloid.]
- EDMONDSON, J. R. *Echium*. In: P. H. DAVIS, ed., *Fl. Turkey* **6**: 318–324. 1978. [Nine species recognized.]
- ESAU, K., & J. THORSCH. Nuclear crystalloids in sieve elements of species of *Echium* (Boraginaceae). *Jour. Cell Sci.* **54**: 149–160. 1982. [Occurrence of crystalloids in developing nuclei of sieve-tube elements in 15 species of *Echium*.]
- FERNANDES, R. B. Quelques notes sur le genre *Echium* L. *Bol. Soc. Brot.* **43**: 145–158. pls. 1–4. 1969. [Nomenclatural notes and synonymies of two species; subspecies, varieties, and forms recognized within *E. creticum*.]
- FRITSCH, B. Karyologische Untersuchungen in der Gattung *Echium* L. (English summary.) *Bot. Not.* **126**: 450–458. 1973. [Chromosome numbers of 12 species and karyotypes of four; literature survey of chromosome numbers for the genus.]
- GIBBS, P. E. Taxonomic studies on the genus *Echium*. I. An outline revision of the Spanish species. *Lagascalia* **1**: 27–82. 1971. [Fifteen species; key, descriptions, distributions, illustrations, maps.]
- . *Echium*. In: T. G. TUTIN, et al., eds., *Fl. Europaea* **3**: 97–100. 1972. [Eighteen species recognized.]

- GIESECKE, P. R. Serum biochemistry in horses with *Echium* poisoning. Austral. Vet. Jour. **63**: 90, 91. 1986. [Poisoning by pyrrolizidine alkaloids from feeding on *E. Lycopsis*.]
- HITCHCOCK, A. S., & M. L. GREEN. Standard-species of Linnean genera of Phanerogamae (1753–1754). Pp. 111–199 in Internatl. Bot. Congress, Cambridge, England, 1930. Nomenclature. Proposals of British Botanists. London. 1929. [*Echium*, 128.]
- INOUE, H., H. MATSUMURA, M. KAWASAKI, K. INOUE, M. TSUKADA, & M. TABATA. Two quinones from callus cultures of *Echium Lycopsis*. Phytochemistry **20**: 1701–1705. 1981. [*E. plantagineum*, production of several root pigments in tissue cultures.]
- JAHANDIEZ, E., & R. MAIRE. Catalogue des plantes du Maroc. 913 pp. Algeria. 1931–1934. [*Echium*, 603–609; 25 species recognized.]
- JOHNSTON, I. M. Studies in the Boraginaceae, XXV. A revaluation of some genera of the Lithospermeae. Jour. Arnold Arb. **34**: 258–299. 1953. [*Echium*, 283–293; detailed generic description, generic limits, variation of characters, taxonomic difficulties.]
- KIRK, W. D. J. Ecological studies on *Thrips imaginis* Bagnall (Thysanoptera) in flowers of *Echium plantagineum* L. in Australia. Austral. Jour. Ecol. **9**: 9–18. 1984.
- KLOTZ, G. Übersicht über die im Botanischen Garten zu Halle (Saale) kultivierten *Echium*-Arten. Wiss. Zeitschr. Martin-Luther Univ. Halle **5**: 335–341. 1955. [Twenty species; origin, descriptions, key, illustrations.]
- . Die in der UdSSR vorkommenden *Echium*-Arten. *Ibid.* **9**: 363–377. 1960. [Five species; key, descriptions, synonymy, illustrations, maps.]
- . Zur Systematik und Nomenklatur einiger *Echium*-Arten I. *Ibid.* **11**: 293–302. 1962a. [Parts II and III in *Ibid.* 703–711 and 1087–1103, respectively; descriptions, extensive synonymy, keys, illustrations, distributions, maps.]
- . Die *Echium*-Arten der ČSSR. *Ibid.* **12**: 137–142. 1962b. [Four species; key, descriptions, distributions, maps.]
- KUNKEL, G. *Echium* × *Lemsii* hybr. nov. y una nota sobre *Scrophularia auriculata* en Gran Canaria. (English summary.) Cuad. Bot. Canar. **28**: 13–16. 1977. [Putative parents are *E. Decaisnei* and *E. strictum*.]
- KUNKEL, M. A., & G. KUNKEL. Iconografía: *Senecio Hansenii*/*Echium* × *Lidii*. Cuad. Bot. Canar. **28**: 31–34. 1977. [Putative parents are *E. Decaisnei* and *E. virescens*.]
- LACAITA, C. C. A revision of some critical species of *Echium*, as exemplified in the Linnean and other herbaria; with a description of *Echium judaeum*, a new species from Palestine. Jour. Linn. Soc. Bot. **44**: 363–438. 1919. [Species of *Echium* in the herbaria of Jussieu, Lamarck, Linnaeus, Sibthorp, and Tournefort, as well as those listed in the eighth edition of Miller's dictionary.]
- LEMS, K., & C. M. HOLZAPFEL. Evolution in the Canary Islands. I. Phylogenetic relations in the genus *Echium* (Boraginaceae) as shown by trichome development. Bot. Gaz. **129**: 95–107. 1968a. [Twenty-three species; trichome types, life zones, evolutionary relationships based on trichome morphology.]
- & ———. Evolution in the Canary Islands. II. Revision of the annual and biennial species of *Echium* (Boraginaceae). Bull. Torrey Bot. Club **95**: 37–57. 1968b. [Four species; illustrations, descriptions, maps, key.]
- & ———. Adaptation of growth form in *Echium leucophaeum* (Boraginaceae). Ecology **52**: 499–506. 1971a. [Altitudinal and ecotypic differentiation, comparison with garden-grown plants.]
- & ———. Botanical notes on Canary Islands. IV. *Echium Decaisnei*-*Echium Famarae* complex (Boraginaceae). Inst. Nac. Invest. Agrar. An. Ser. Prod. Veg. **1**: 189–196. map. 1971b.*
- LEREBDE, C. Sur la position des étamines chez quelques *Echium*. Bull. Soc. Hist. Nat. Toulouse **90**: 369–372. 1955. [*E. plantagineum*, *E. vulgare*.]

- LITARDIÈRE, R. DE. Recherches caryologiques et caryo-taxonomiques sur les Boraginacées. II. Nombres chromosomiques dans le genre *Echium*. Boissiera 7: 155-165. 1943. [Chromosome counts for 21 species; see FRITSCH.]
- LUQUE, T. Estudio cariológico de Boragináceas Españolas. II. *Echium* L. de España peninsular e Islas Baleares. (English summary.) Lagasalia 13: 17-38. 4 pls. 1984. [Chromosome counts for 16 (as 18) species, karyotypes, polyploidy.]
- MALECKA, J. The course of differentiation of the endosperm of *Echium vulgare* L. Acta Biol. Cracov. Bot. 18: 13-26. 2 pls. 1975.
- NICHOLLS, M. S. Spatial pattern of ovule maturation in the inflorescence of *Echium vulgare*: demography, resource allocation and the constraints of architecture. Biol. Jour. Linn. Soc. 31: 247-256. 1987.
- OLESEN, J. M. Floral biology of the Canarian *Echium Wildpretii*: bird-flower or a water resource to desert bees? Acta Bot. Neerl. 37: 509-513. 1988. [Reproductive biology, UV-pattern of flowers, bee and bird pollination.]
- PERIS, J. B., R. FIGUEROA, & G. STÜBING. A new species of *Echium* for the Spanish flora. Bot. Jour. Linn. Soc. 97: 261-266. 1988. [*E. saetabense*, sp. nov.; illustrations, differences from *E. italicum* and *E. flavum*.]
- PERRY, G., & J. MCNEIL. Proposal to reject the name *Echium Lycopsis* L. (Boraginaceae) with notes on the correct name for the weed Paterson's Curse (purple viper's bugloss). Taxon 36: 483-492. 1987.
- PIGGIN, C. M. Factors affecting seed germination of *Echium plantagineum* and *Trifolium subterraneum*. Weed Res. 16: 337-344. 1976.* [Related papers in *Ibid.* 267-272; 17: 361-366. 1977; 18: 9-18. 1978.]
- . The herbaceous species of *Echium* (Boraginaceae) naturalized in Australia. Muelleria 3: 215-244. 1977. [*E. italicum*, *E. plantagineum*, *E. vulgare*; descriptions, distributions, key, maps.]
- . Dispersal of *Echium plantagineum* by sheep. Weed Res. 18: 155-160. 1978.* [A related paper on flowering and seed production in *Ibid.* 83-88.]
- . The biology of Australian weeds: 8. *Echium plantagineum* L. Jour. Austral. Inst. Agr. Sci. 48: 3-16. 1982.*
- PUSATERI, W. P., & W. H. BLACKWELL, JR. Taxonomy, distribution, and historical considerations of *Echium* (Boraginaceae) in North America. (Abstr.) ASB Bull. 25(2): 62. 1978.
- & ———. The *Echium vulgare* complex in eastern North America. Castanea 44: 223-229. 1979. [Evaluation of infraspecific taxonomy, variation, economic importance.]
- QAISER, M. Boraginaceae. In: S. M. H. JAFRI & A. EL-GADI, eds., Fl. Libya 68: 1-95. 1979. [*Echium*, 12 species, 33-49.]
- ST. GEORGE-GRAMBAUER, T. D. Hepatogenous chronic copper poisoning in sheep in South Australia due to the consumption of *Echium plantagineum* L. Austral. Vet. Jour. 38: 288-293. 1962.*
- SENNEN, F. Diagnoses des nouveautés parues dans les exsiccata plantes d'Espagne et du Maroc. 308 pp. 1936. [Descriptions of 21 "new" species from Morocco and four from Spain.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez l'*Echium vulgare* L. Compt. Rend. Acad. Sci. Paris 207: 871, 872. 1938.
- SPRAGUE, T. A., & J. HUTCHINSON. *Echiums* from the Atlantic Islands. Bull. Misc. Inf. Kew 1914: 116-122, 265-267. 3 pls. 1914. [Descriptions, nomenclature, sectional classification, new taxa, illustrations, keys.]
- TABATA, M., M. TSUKUDA, & H. FUKUI. Antimicrobial activity of quinone derivatives from *Echium Lycopsis* callus cultures. Pl. Med. 44: 234-236. 1982. [Quinones inhibit growth of gram-positive bacteria.]
- VALSECCHI, F. Contribution to the knowledge on the genus *Echium*: I. The *Echium* of Sardinia. (In Italian; English summary.) Webbia 32: 101-127. 1977. [Eight species; descriptions, distributions, illustrations, key.]

- VERESHCHAGINA, V. A. Microsporogenesis in the gynodioecious *Echium vulgare* L. (In Russian.) Bot. Zhur. **56**: 1006–1013. 1971.
- . Some special embryological features of the gynodioecious species of the genus *Echium* (Boraginaceae). (In Russian.) *Ibid.* **61**: 1582–1589. 1976. [*E. russicum*, *E. vulgare*.]
- . Study of the gynodioecy in *Echium amoenum* (Boraginaceae). 1. Flowering and pollination. (In Russian; English summary.) *Ibid.* **63**: 183–190. 1978.
- & O. M. ERMISHINA. The study of meiosis in microsporocytes of sex flower forms of *Echium russicum* J. F. Gmelin (Boraginaceae). (In Russian.) *Ibid.* **58**: 1760–1764. 1973.
- WOOD, H., & R. DEGABRIELE. Genetic variation and phenotypic plasticity in populations of Paterson's Curse (*Echium plantagineum* L.) in southeastern Australia. Austral. Jour. Bot. **53**: 677–685. 1985.

Tribe 5. BORAGINEAE

16. *Borago* Linnaeus, Sp. Pl. **1**: 137. 1753; Gen. Pl. ed. 5. 67. 1754.

Annual [or perennial] hispid, hirsute, or setose herbs. Stems erect [or decumbent], coarse [or slender]. Trichomes of various sizes, the coarser ones usually bulbous at base, often sparsely mixed with minute, glandular, papilla-like trichomes. Lower leaves petiolate, upper ones sessile, usually amplexicaul. Inflorescences branched, lax, bracteate, raceme-like cymes; flowers long pedicellate, usually nodding. Calyx 5 lobed, divided almost to the base, accrescent in fruit, the lobes linear-lanceolate, usually hirsute. Corolla rotate [to broadly campanulate], blue, pink, or rarely white; tube obsolete [or very short]; lobes imbricate, lanceolate, acute at apex; faucal appendages 5, alternate with stamens, inserted at the throat, emarginate, glabrous, exserted. Stamens 5, exserted; filaments inserted near base of corolla tube, extended into a long, narrow appendage beyond the insertion of anthers; anthers linear, connivent, mucronate, introrse, forming a conical structure. Ovary deeply divided into 4 one-ovulate lobes; style gynobasic, long, filiform; stigma capitate, entire. Nutlets 4, erect, oblong to ovoid, longitudinally ribbed [or not], rugose-muricate [or smooth]; areola with a conspicuous thickened, collarlike rim that surrounds a markedly protruding caruncle-like plug; gynobase flat or weakly concave. Base chromosome number 8. (Including *Buglossites* Moris & Notaris, non Bubani.) TYPE SPECIES: *B. officinalis* L., the only species in the protologue. (Name believed to be of Medieval Latin origin of unknown derivation.)—BORAGE.

A well-marked genus of four Mediterranean species, of which *Borago longifolia* Poiret is endemic to Algeria, *B. Trabutii* Maire to Morocco, and *B. pygmaea* (DC.) Chater & Greuter to Capraia, Corsica and Sardinia. The fourth species, *Borago officinalis* L., borage, $2n = 16$, is cultivated as an ornamental or medicinal plant throughout most of the world; it has often escaped from cultivation. It is a sporadic weed in North America and has been reported from the Southeastern States only from Tennessee (Fernald; Johnston, 1924a). The record is almost certainly based on Gatterer. It is with some doubt that *Borago* is

included in this account, since it is uncertain whether *B. officinalis* is really established anywhere in the Southeast.

Borago is easily distinguished from the remainder of the subfamily Boraginoideae in having a rotate or rarely broadly campanulate, usually blue corolla with emarginate faucal appendages; appendiculate staminal filaments and apiculate, linear, connivent, exerted anthers; a flat receptacle with pitlike scars left by the nutlets, and erect, muricate nutlets with an annular basal rim and a well-developed, caruncle-like plug. In their rotate corollas and erect, connivent, linear anthers, the flowers of *Borago* superficially resemble those of *Solanum* L.

Each of the species of *Borago* was placed in a monotypic section by De Candolle. His sectional classification was followed by Gürke and later by Popov (1953) but has been ignored by most other students of the Boraginaceae. Guşuleac (1931) raised two of De Candolle's sections to subgenera and reduced the third to synonymy. He placed *B. pygmaea* (as *B. laxiflora*) in the monotypic subg. *Buglossites* (Moris & Notaris) Guşuleac, which he distinguished from subg. *Borago* (as *Euborago*), which included the remaining three species of the genus, by its funnellform corolla with small, transversely linear scales, instead of a rotate corolla with large, emarginate scales.

Plants of *Borago officinalis* have a polygenic reproductive system that ranges from fully self-incompatible to self-compatible. Heterozygous plants are self-compatible, but the level of self-compatibility declines as the number of homozygous gene loci increases. Crowe suggested that complete self-incompatibility results from the presence of a certain critical number of homozygous gene loci.

The flowers of *Borago officinalis* are protandrous and are pollinated primarily by various kinds of bees. Because the flowers are nodding, the bee hangs upside down by grasping the toothlike appendages of the staminal filaments and inserting its proboscis between the anthers. As a result, the conical structure formed by the connivent anthers is displaced, and the lower surface of the bee receives a pollen shower.

Pollen of *Borago officinalis* is isopolar, usually subprolate, zonocolporate, and often with ten (rarely nine or twelve) colpi and a conspicuous girdle. The colpi (ectoapertures) are narrow, and the endoapertures fuse with each other into an equatorial girdle. The tectum is characterized by perforations and is densely gemmate. The surface of the gemmae is finely sculptured (Saad-Limam & Nabli).

Chromosome numbers have been reported for all species of *Borago* (Contandriopoulos; Diana-Corrias; Strey). *Borago pygmaea* is tetraploid ($2n = 32$), whereas *B. longifolia*, *B. officinalis*, and *B. Trabutii* are diploid ($2n = 16$). It is interesting that the first species and the last three fall in Guşuleac's (1931) subgenera *Buglossites* and *Borago* (*Euborago*), respectively. D'Amato & Marchi showed that the karyotype of *B. officinalis* consists of six pairs of metacentric chromosomes (one with satellites) and two of submetacentric chromosomes.

The flowers and seeds of *Borago officinalis* contain a saturated pyrrolizidine alkaloid, thesinine, whereas the leaves contain the unsaturated alkaloids amabiline and lycopsamine. Saturated pyrrolizidines

are not known to be toxic, but the unsaturated ones are suspected of being hepatotoxic (Dodson & Sternitz; Larson *et al.*). The seeds of *B. officinalis* contain high concentrations (37 and 20 percent, respectively) of linoleic and 6,9,12 octadecatrienoic acid and only a trace (0.9 percent) of linolenic acid (Kleiman *et al.*).

Of the numerous species of Boraginaceae surveyed for cyanogenic compounds, only *Borago officinalis* has tested positive. It contains the glycoside dhurrin and is known to release hydrocyanic acid (Valen). Gibbs did not detect cyanogens in *B. pygmaea* (as *B. laxiflora*).

Borago officinalis is cultivated as an ornamental and is used as a potherb. The chopped leaves are said to give salad a flavor of cucumber; the leaves have also been eaten as a substitute for spinach. The flowers are used in the decoration of cakes, in the preparation of tea and candied blossoms, and in the flavoring of wines and other drinks. Infusions prepared from the plant were primarily used as a demulcent, diaphoretic, and refrigerant (Youngken), and decoctions, crushed plants, and emollients were used in the treatment of tumors (Hartwell).

REFERENCES:

- Under family references see AL-NOWAIHI *et al.*; BACIU; BAILEY *et al.*; BAILLON; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; DE CANDOLLE; G. C. S. CLARKE; DíEZ (1984); FELL & PECK; FERNALD; FERNANDES & LEITÃO; GATTINGER; GIBBS; GLEASON; GÜRKE; HARTWELL; HEDRICK; HEGI; HOFMANN *et al.*; JODIN; JOHNSTON (1924a, 1927); KERNER VON MARILAUN; KLEIMAN *et al.*; KNUTH; LEWIS & ELVIN-LEWIS; LOEW; LUBBOCK; MANSFELD; J. S. MILLER; MITCHELL & ROOK; NASH & MORENO; NEUBAUER; POLLARD & AMUTI; POPOV (1953); RIDLEY; SAHAY; SCHAEFER; SHARP *et al.*; SINGH; STREY; SYNGE; TÉTÉNYI; TOELKEN; UPHOF; VALEN; WILLAMAN & LI; YOUNGKEN; and ZEVAN & DE WET.
- CHATER, A. O. *Borago*. In: T. G. TUTIN *et al.*, eds., *Fl. Europaea* 3: 109. 1972. [*B. officinalis*, *B. pygmaea*.]
- & W. GREUTER. *Borago laxiflora*. In: V. H. HEYWOOD, ed., *Flora Europaea notulae systematicae ad floram Europaeam spectantes*. Bot. Jour. Linn. Soc. 65: 223–269. 1972. [*B. pygmaea*, 260, 261.]
- CONTANDRIOPOULOS, J. Contribution à l'étude caryologique des endémiques de la Corse. Ann. Fac. Sci. Marseille 26: 51–65. 1957. [*Borago*, 57; *B. longifolia*, 2n = 16; *B. officinalis*, 2n = 16; *B. pygmaea* (as *B. laxiflora*), 2n = 32; *B. Trabuttii*, 2n = 16.]
- CROWE, L. K. The polygenic control of outbreeding in *Borago officinalis*. Heredity 27: 111–118. 1971. [Homozygous individuals are self-incompatible, heterozygous ones self-compatible.]
- D'AMATO, G., & P. MARCHI. Heterochromatin in *Borago officinalis* L. (Boraginaceae): comparison between Feulgen and Giemsa stained heterochromatic segments. Ann. Bot. Roma 41: 165–168. 1983. [Karyotype, 2n = 16.]
- DIANA-CORRIAS, S. Numeri cromosomici per la flora Italiana: 701–707. Inform. Bot. Ital. 12: 125–129. 1980. [*B. pygmaea*, 125, 2n = 32.]
- DODSON, C., & F. R. STERNITZ. Pyrrolizidine alkaloids from Borage (*Borago officinalis*) seeds and flowers. Jour. Nat. Prod. 49: 727, 728. 1986. [Flowers and seeds contain thesinine.]
- EDMONDSON, J. R. *Borago*. In: P. H. DAVIS, ed., *Fl. Turkey* 6: 434, 435. 1978. [*B. officinalis*.]

- FELL, K. R., & J. M. PECK. The anatomy of the leaf and flower of *Borago officinalis* L. *Pl. Med.* **16**: 29–42. 1968. [History and medicinal uses; detailed account of anatomy and morphology.]
- FRANZ, G. Untersuchungen über die Schleimpolysaccharide von *Tussilago Farfara* L., *Symphytum officinale* L., *Borago officinalis* L. und *Viola tricolor* L. (English summary.) *Pl. Med.* **17**: 217–220. 1969. [Mucilage content.]
- GILL, S. Chromosome numbers in West-Himalayan bicarpellate species II. *Bull. Torrey Bot. Club* **99**: 36–38. 1972. [*B. officinalis*, $n = 8$.]
- GUŞULEAC, M. Die monotypischen und artenarmen Gattungen der Anchuseae. *Repert. Sp. Nov. Regni Veg.* **29**: 113–125. 1931. [*Borago*, 120–125, pls. 113, 114; two subgenera and four species recognized.]
- . Zur ökologischen Morphologie der Blüte von *Borago officinalis* nebst phylogenetischen Betrachtungen. *Rev. Biol.* **5**: 169–175. 1960.
- JYUROVAT, G. G. Borage for courage. *Herbarist* **39**: 50–53. 1973. [*B. officinalis*, uses.]
- LARSON, K. M., M. R. ROBY, & F. R. STERMITZ. Unsaturated pyrrolizidines from Borage (*Borago officinalis*), a common garden herb. *Jour. Nat. Prod.* **47**: 747, 748. 1984. [Containing lycopsamine and supinidine viridiflorate.]
- QUINN, J. T., J. E. SIMON, & J. JANICK. Somatic embryogenesis in *Borago officinalis* L. *HortScience* **22**: 1130. 1987. [Somatic embryos obtained by culturing immature zygotic embryos on a basal medium containing salts, vitamins, coconut water, and 2,4-D.]
- , A. WHIPKEY, J. SIMON, & J. JANICK. Embryo development in *Borago officinalis*. (Abstr.) *HortScience* **21**: 784. 1986. [Development and content of linolenic acid in sexual and asexually produced embryos.]
- QUIROZ-GARCÍA, D. L., & R. PALACIOS-CHÁVEZ. Catálogo palinológico para la flora de Veracruz. No. 21. Familia Boraginaceae. Género *Borago*. (English summary.) *Biotica* **10**: 67–70. 1985. [*B. officinalis*.]
- SAAD-LIMAN, S. B., & M. A. NABLI. Ultrastructure of the exine of *Borago officinalis* (Boraginaceae). *Grana* **23**: 1–10. 1984. [Transmission and scanning electron microscopy.]
- SAUPE, S. G. Cyanogenic compounds and angiosperm phylogeny. Pp. 80–116 in D. A. YOUNG & D. S. SEIGLER, eds., *Phytochemistry and angiosperm phylogeny*. New York. 1981. [*B. officinalis*, 89.]
- SPRAGUE, T. A. The correct spelling of certain generic names: II. *Bull. Misc. Inf. Kew* **1928**: 285–296. 1928. [*Borago* or *Borrigo*, 288–292.]
- STIX, E. Pollenmorphologie von *Borago officinalis* L. *Grana Palyn.* **5**: 24–32. 1964.
- TACINA, F. Ultrastructure of nectariferous cells of *Borago officinalis* L. (In French.) *Rev. Roum. Biol. Ser. Bot.* **17**: 227–234. 1972.
- THEIMER, R. R., & R. SCHUSTER. Light-dependent inhibition of germination and early seedling development of *Borago officinalis*. *Zeitschr. Pflanzenphysiol.* **90**: 111–118. 1978.
- WHIPKEY, A., J. E. SIMON, & J. JANICK. In vivo and in vitro lipid accumulation in *Borago officinalis* L. *Jour. Am. Oil Chem. Soc.* **65**: 979–984. 1988. [Seed fatty acids of 13 samples; average concentrations of linoleic and linolenic, oleic and palmitic acids are 38.1, 22.8, 16.3, and 11.3 percent, respectively.]

17. *Symphytum* Linnaeus, *Sp. Pl.* **1**: 136. 1753; *Gen. Pl.* ed. 5. 66. 1754.

Perennial, usually hispid herbs. Rootstocks fusiform [rhizomatous, or stoloniferous], not fleshy [or tuberous]. Stems branched [or simple] at base, winged or wingless, softly hairy and hispid [or with retrorse,

rigid, prickly-like trichomes]. Basal leaves long-petiolate, lanceolate, ovate [or cordate], entire. Uppermost cauline leaves sessile [or petiolate], decurrent [or not] at base. Inflorescences ebracteate, terminal, scorpioid cymes, elongated in fruit. Calyx persistent, 5 lobed, divided to the base [or divided as little as one-sixth its length], campanulate [to tubular], usually accrescent in fruit, densely hairy. Corolla purplish, pink, white [or yellowish], narrowly funnelform [to tubular], usually much enlarged distally, pubescent on the outside; limb equalling [or shorter than] tube, the lobes reflexed [or straight], triangular [or linear], shorter [or longer] than remainder of limb; throat with 5 well-developed faucal appendages, these included [or exserted], linear-lanceolate [to subulate], papillose, often with converging tips. Stamens 5, usually included; filaments short; anthers oblong with connectives usually extending beyond thecae. Ovary deeply 4 lobed, 4 ovulate; style filiform, gynobasic, usually long exserted. Nutlets 4 (or fewer by abortion), ovoid, oblique [or straight], suberect [erect, or horizontal], black [or brown to grayish], smooth and glossy [rugose, tuberculate, or verruculose], usually obliquely keeled, with a well-differentiated basal attachment-ring; ring collar-like, marginally toothed, the teeth clasping the receptacle; caruncle protruding. Base chromosome numbers 8, 10, 12, 14-16. (Including *Procoptantia* Guşuleac.) LECTOTYPE SPECIES: *S. officinale* L.; see Britton & Brown, *Illus. Fl. No. U.S. & Canada*, ed. 2, **3**: 92, 1913. (Name from Greek *symphyton*, grown together, denoting the reputed healing virtues of the plants, as indicated by the decurrent leaves [Fernald].)—COMFREY.

A well-defined Old World genus of about 35 species distributed primarily in Turkey (20 species, nine endemic), the Caucasus (11 species, four endemic), and the Balkan Peninsula and Aegean Islands (11 species, four endemic). *Symphytum* is poorly represented in Europe and Central Asia and apparently has no indigenous taxa beyond those continents. The genus is represented in North America by three naturalized species and in the southeastern United States by one.

Symphytum officinale L. (*S. bohemicum* Schmidt, *S. tanaicense* Steven, *S. uliginosum* Kerner), common comfrey, healing herb, $2n = 24, 32, 40-48, 56$, is a coarse, densely pilose-hispid perennial with decurrent cauline leaves, recurved corolla lobes, and glossy, smooth nutlets. It is a European plant cultivated and naturalized in North America, where it grows in disturbed sites, waste places, old fields, and thickets, as well as along roadsides. It has apparently escaped from cultivation in Arkansas (Smith, 1978, 1988) and Tennessee (Gattinger, Small, 1933). Although Britton & Brown, Gadella (1984), Johnston (1924a), and Small (1903, 1933) listed *S. officinale* from North Carolina, Hommersand did not include it in the flora of that state. Similarly, the species was said to occur in Georgia (Fernald; Gadella, 1984; Rickett; Steyermark) but was not included in Jones & Coile's distributional account of the vascular flora of that state. Because of its medicinal

attributes and ornamental value, the species is probably cultivated in all of the Southeastern States.

The Eurasian *Symphytum asperum* Lepechin and *S. tuberosum* L. are also naturalized in North America (Fernald; Gadella, 1984; Gleason), but neither one has been reported from the southeastern United States.

Bucknall's division of *Symphytum* into two "subgenera" and seven sections has since been amended by Gviniashvili (1969, 1972a), Pawlowski (1961, 1971), and Wickens (1969). As many as ten sections and several series are now recognized. Because *Symphytum* is represented in the Southeastern States by only a single introduced species that belongs to sect. SYMPHYTUM, the entire sectional classification of the genus will not be reviewed here.

Symphytum has always been placed in the tribe Boragineae (including the Anchuseae). It is readily distinguished from other members of that tribe in being perennials with well-developed rhizomes, ebracteate cymes, elongated faucal appendages, funnellform or tubular corollas, and nutlets with a basal, collar-like attachment ring. Pawlowski (1971b, 1972) maintained *Procopiania* as distinct from *Symphytum* on the basis of its having long-exserted stamens and corolla lobes longer than the tube. However, Runemark concluded that morphological, cytological, and palynological data support uniting the two genera. Wickens reduced *Procopiania* to a section of *Symphytum*.

Chromosome numbers are known for 16 species (ca. 46 percent of the total). Grau suggested that the primitive base number for the genus is 12, from which lower ($x = 10$) and higher ($x = 14, 15, 16$) base numbers were derived. Aneuploidy and polyploidy apparently have played an important role in the evolution of the genus. Decaploids based on 12 have been reported for *S. bulbosum* Schimper and *S. cordatum* Waldst. & Kit. ex Willd., and dodecaploids ($2n = 144$) are known in *S. tuberosum* (Grau, 1968). The last species also has hexaploid, heptaploid, and octoploid numbers based on 12, but Tarnauschi (1948; see Bolkhovskikh *et al.*) reported $2n = 18$, a number that has not been observed by other workers. Diploid and tetraploid counts (based on 12), as well as aneuploids ($2n = 40-47$) have been found in *S. officinale*. The 12 pairs of chromosomes of the diploid *S. officinale* can be distinguished morphologically by using the Feulgen-Giemsa banding technique (Mekki *et al.*).

Natural interspecific hybridization has been well documented in *Symphytum*. Bucknall (1912, 1913) assigned names to hybrids between several pairs of species, but he gave different names to hybrids involving different varieties of a given species pair. The hybrid origin of *S. ×uplandicum* Nyman ($2n = 40$) from *S. officinale* ($2n = 48$) and *S. asperum* ($2n = 32$) was established by Gadella & Kliphuis (1973), and the natural and synthetic interspecific hybrids were remarkably similar. *Symphytum ×uplandicum* derived from *S. officinale* with $2n = 40$ has a chromosome number of $2n = 36$. The chromosome number in the hybrid is further complicated as a result of backcrossing to *S.*

officinale, and five hybrid races with $2n = 34, 36, 40, 42$, and 44 have been reported (Gadella & Kliphuis, 1975). Both $2n = 36$ and $2n = 40$ cytological types of *S. ×uplandicum* have been introduced into North America (Gadella, 1984). Basler reported that although meiotic disturbance in *S. ×uplandicum* is about 14 percent, pollen fertility is more than 95 percent. The hybrid is genetically stable, and it bridges, via backcrossing, the morphological and cytological gap between the parental species. Interspecific hybrids between *S. orientale* and both *S. officinale* and *S. ottomanum* Frivald have been reported by Kurtto (1981, 1985, respectively). Intraspecific hybrids between diploid and tetraploid cytotypes of *S. officinale* are known (Basler; Gadella & Kliphuis, 1972). The hybrid between *S. icaricum* Paw. (probably a subspecies of *S. Davisii* Wickens; see Stearn) and *S. circinale* Runemark was recognized by Pawlowski (1971b) as an intergeneric one, since he placed the latter species in the segregate *Procopia*.

The presence of triterpene and pyrrolizidine alkaloids was employed by Gadella *et al.* (1983) and Huizing *et al.* (1982, 1983) to elucidate the hybrid origin of *Symphytum ×uplandicum* from *S. asperum* and *S. officinale*. These authors found that the alkaloid echimidine is present in *S. asperum* and *S. ×uplandicum* but not in any of the cytotypes of *S. officinale*. They also isolated the triterpene isobaueranol from *S. officinale* and the hybrid, but not from *S. asperum*. However, Jaarsma *et al.* found that such a sharp chemical differentiation is not always absolute, and there are some anomalies in the chemical profiles within the *S. officinale* complex. In fact about 25 percent of the samples of *S. officinale* were found to contain traces of echimidine. As many as seven alkaloids have been isolated from *S. asperum* (Roitman) and eight from *S. ×uplandicum* (Culvenor *et al.*, 1980a).

Knuth listed numerous pollinators of the flowers of seven species of *Symphytum*. The corolla throat in the genus is closed by a conical structure made up of the five anthers and the five alternating faucal appendages. Nectar accumulating at the base of the corolla is "legitimately" accessible to insects with a proboscis longer than 1 cm. However, several species of bees with a short proboscis have been observed "stealing" nectar by piercing holes or slits at the base of the corolla tube. The flowers of many species of *Symphytum* are drooping, and pollen falling from the anthers to the long-exserted stigmas ensures self-pollination.

Pollen of *Symphytum* is (7-)8-10(-11) zonocolporate, prolate or dumbbell shaped, rounded at the poles, and with short, narrow colpi and circular pores (Ahn & Lee; Clarke; Sahay).

Elaiosomes on the nutlets of species of *Symphytum* have been suspected of aiding in its dispersal by ants (Bresinsky).

Several species of *Symphytum* are cultivated as ornamentals (Bailey *et al.*; Ingram), but the genus has long been considered to be a valuable source of medicinal plants, which have been used by herbalists for 2000 years (Wilkes). The advantages of the common comfrey (*S. officinale*) and Russian comfrey (*S. ×uplandicum*) have been listed in great detail

by Hills (1975, 1976), Kadans, Mathieu, and Uphof. These plants have been said to cure pulmonary and scrofular diseases, diarrhea, colds, coughs, sores, calcium deficiency, asthma, arthritis, hemorrhoids, gout, gangrene, burns, anemia, gastric and duodenal ulcers, bloody urine, cuts and wounds, headaches, and tuberculosis, as well as to be useful in protection of the skin. Furthermore, preparations from the rhizomes and/or roots have been recommended to relieve pain from stings of bees and bites of mosquitos and horseflies, as well as from itching caused by chicken pox, contact dermatitis, and psoriasis. The plants have been widely grown as green feed for hogs, goats, sheep, rabbits, and cows, and the young plants are consumed by man as a salad plant and in the preparation of tea.

A very serious health concern about the consumption of *Symphytum* by man and domesticated animals has been raised by Culvenor *et al.* (1980), Mattocks, and Roitman. These authors have indicated that comfrey causes hepatotoxicity and even liver cancer in rats. Since the toxic effects of pyrrolizidine alkaloids appear after a long period of limited consumption, these authors have recommended very strongly that comfrey should not be consumed.

REFERENCES:

- Under family references see AHN & LEE; AL-NOWAIHI *et al.*; BACIU; BAILEY *et al.*; BAILLON; BATE-SMITH; BELVAL & EVIN; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BOURDU; BRESINSKY; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; I. H. BURKILL; DE CANDOLLE; G. C. S. CLARKE; EVERIST; FABRE; FELL & PECK; FERNALD; FERNANDES & LEITÃO; GATTINGER; GLEASON; GOLDBLATT (1981, 1984, 1985, 1988); GRAU (1968); GÜRKE; HEDRICK; HEGI; HOFMANN *et al.*; HOMMER-SAND; INGRAM; ISHIKURA; JAMIESON & REID; JODIN; JOHNSTON (1924a, b); KERNER VON MARILAUN; KNUTH; LOEW; MACROBERTS; MANSFIELD; MARKOVA & IVANOVA (1970); MITCHELL & ROOK; MOERMAN; R. J. MOORE (1973, 1974, 1977); MÜLLER; MUENSCHER; POLLARD & AMUTI; POPOV (1953); RICKETT; RIDLEY; RIEDL (1967); SAHAY; SAUER & SAUER; SCHAEFER; SHARP *et al.*; SMALL (1903, 1933); E. B. SMITH (1978, 1988); SMITH & CULVENOR; STEYERMARK; STREY; SYNGE; TÉTÉNYI; UPHOF; WILLAMAN & LI; WILLAMAN & SCHUBERT; YOUNGKEN; and ZEVAN & DE WET.
- BASLER, A. Cytotaxonomische Untersuchungen an der Boraginaceen-Gattung *Symphytum* L. Untersuchungen an überwiegend norddeutschen Pflanzen der Arten *S. asperum* Lepech., *S. officinale* L. und *S. xuplandicum* Nym. (English summary.) Bot. Jahrb. **92**: 508–553. 1972. [Chromosome numbers from 48 populations; allopolyploidy, meiotic irregularities, backcrosses.]
- BEHNINGER, C., G. ABEL, E. RÖDER, V. NEUBERGER, & W. GÖGGMANN. Wirkung eines Alkaloidextraktes von *Symphytum officinale* auf menschliche Lymphocytenkulturen. (English summary.) Pl. Med. **55**: 518–522. 1989. [Alkaloid extracts at concentrations of 140 µg/ml and higher caused chromosomal aberrations.]
- BOURDU, R. Sur les glucosides de *Symphytum officinale* L. et leur métabolisme. Compt. Rend. Acad. Sci. Paris **246**: 973–976. 1958.
- BUCKNALL, C. Some hybrids of the genus *Symphytum*. Jour. Bot. London **50**: 332–337. 1912. [Natural interspecific hybrids between *S. officinale* and *S. peregrinum*.]

- . A revision of the genus *Symphytum* Tourn. Jour. Linn. Soc. Bot. **41**: 491–556. 1913. [Twenty-five species; sectional classification, descriptions (in Latin), distributions, synonymies, interspecific hybridizations, keys.]
- BUTLER, G. W., J. D. FERGUSON, & R. M. ALLISON. The biosynthesis of allantoin in *Symphytum*. Physiol. Pl. **14**: 310–321. 1961. [In leaf disks of *S. ×uplandicum*.]
- CHADHA, Y. R., ed. The wealth of India. Vol. 10. *Frontisp.* + xlix + 591 pp. + xxv. New Delhi. 1976. [*Symphytum*, 88, 89.]
- CULVENOR, C. C. J., M. CLARKE, J. A. EDGAR, J. L. FRAHN, M. V. JAGO, J. E. PETERSON, & L. W. SMITH. Structure and toxicity of the alkaloids of Russian comfrey (*Symphytum ×uplandicum* Nyman), a medicinal herb and item of human diet. Experientia **36**: 377–379. 1980a. [Eight alkaloids identified.]
- , J. A. EDGAR, J. L. FRAHN, & L. W. SMITH. The alkaloids of *Symphytum ×uplandicum*, Russian comfrey. Austral. Jour. Chem. **33**: 1105–1114. 1980b.*
- DEGEN, A. VON. Bemerkungen über einige orientalische Pflanzenarten. LXXXIX. Über *Symphytum uliginosum* Kern. Magyar Bot. Lapok **29**: 144–148. 1930.
- DIOMAIUTO-BONNAND, J. L'inflorescence du *Symphytum officinale*: évolution des méristèmes axillaires et devenir du méristème apical. Compt. Rend. Acad. Sci. Paris **262**: 638–641. pl. 1966a.
- . La cyme bipare du *Symphytum officinale*: étude de l'initiation et du développement des premiers bourgeons. Passage à la cyme unipar. *Ibid.* 1081–1083. pl. 1966b.
- . Divers aspects de l'inflorescence du *Symphytum officinale* L. *Ibid.* **264**: 817–820. pl. 1967.
- DOBROCHAEVA, D. N. On taxonomy of the genus *Symphytum* L. I. Section *Symphytum*. (In Ukrainian; English summary.) Ukrain. Bot. Zhur. **25**(5): 33–39. 1968a. [Three species in eastern Europe.]
- . On taxonomy of the genus *Symphytum* L. I. Section *Tuberosa* Buckn. (In Ukrainian; English summary.) *Ibid.* **25**(6): 58–62. 1968b. [Four taxa, a new species.]
- FAEGRI, K. Über die Skandinavien gefundenen *Symphytum*-Arten. Bergens Mus. Årbok **4**: 1–47. 2 pls. 1931. [*S. asperum*, *S. officinale*, and *S. peregrinum* reduced to subspecies of *S. commune*; distributions, illustrations, maps.]
- FELL, K. R., & J. M. PECK. British medicinal species of the genus *Symphytum*. Pl. Med. **16**: 208–216. 1968a. [*S. officinale*, *S. tuberosum*, *S. ×uplandicum*; nomenclature, leaf epidermis, trichome types.]
- & ———. Phytochemical investigations of some species of the Boraginaceae. *Ibid.* 411–420. 1968b. [Allantoin content of leaves of *S. officinale*, *S. tuberosum*, and *S. ×uplandicum*.]
- FRANZ, G. Untersuchungen über die Schleimpolysaccharide von *Tussilago Farfara* L., *Symphytum officinale* L., *Borago officinalis* L. und *Viola tricolor* L. (English summary.) Pl. Med. **17**: 217–220. 1969. [Qualitative and quantitative determination of mucilage in roots of *S. officinale*.]
- FROLOV, Y. M. A new species of the genus *Symphytum* (Boraginaceae) from the Caucasus. Bot. Zhur. **70**: 533, 534. 1985. [*S. podcunicum*, sp. nov.]
- & N. P. FROLOVA. Pollination biology and seed formation in prickly comfrey *Symphytum asperum*. Rastit., Resur. **17**: 413–420. 1981.*
- FURUYA, T., & K. ARAKI. Studies on constituents of crude drugs. I. Alkaloids of *Symphytum officinale* Linn. Chem. Pharm. Bull. Japan **16**: 2512–2516. 1968. [Separation and characterization of three root alkaloids.]
- & M. HIKICHI. Alkaloids and triterpenoids of *Symphytum officinale*. Phytochemistry **10**: 2217–2220. 1971. [The alkaloids echimidine and symphytine, the triterpenoid isobauerenol, and β -sitosterol identified from roots.]
- GADELLA, T. W. J. Cytological and hybridization studies in the genus *Symphytum*. Pp. 189–199 in G. VIDA, ed., Evolution in plants. Symposia Biol. Hungarica. Vol. 12. Budapest. 1972. [*S. officinale*, *S. ×uplandicum*; chromosome

- numbers, crossing relationships, distribution, colored plate of flowers of various taxa.]
- . Variatie en hybridisatie bij enkele taxa van het genus *Symphytum*. (English summary.) *Gorteria* 9: 88–93. 1978. [Hybridization between *S. officinale* and *S. ×uplandicum*.]
- . Notes on *Symphytum* (Boraginaceae) in North America. *Ann. Missouri Bot. Gard.* 71: 1061–1067. 1984. [*S. asperum*, *S. officinale*, *S. tuberosum*, *S. ×uplandicum*; chromosome numbers, distributions, key.]
- & E. KLIPHUIS. Cytotaxonomic studies in the genus *Symphytum*, I. *Symphytum officinale* L. in the Netherlands. *Proc. Nederl. Akad. Wet. C.* 70: 378–391. 1967. [Cytogeography, morphology, flowering.]
- & ———. Cytotaxonomic studies in the genus *Symphytum*, II. Crossing experiments between *Symphytum officinale* L. and *Symphytum asperum* Lepech. *Acta Bot. Neerl.* 18: 544–549. 1969. [Successful artificial hybridization between *S. asperum* and the three cytotypes of *S. officinale*.]
- & ———. Cytotaxonomic studies in the genus *Symphytum*, III. Some *Symphytum* hybrids in Belgium and the Netherlands. *Biol. Jaarb. Dodonaea (Gent)* 39: 97–107. 1971.*
- & ———. Cytotaxonomic studies in the genus *Symphytum*, IV. Cytogeographic investigations in *Symphytum officinale* L. *Acta Bot. Neerl.* 21: 169–173. 1972. [Chromosome numbers for 109 populations in Europe; polyploidy, hybridization between plants with different ploidy levels.]
- & ———. Cytotaxonomic studies in the genus *Symphytum*, V. Some notes on W. European plants with the chromosome number $2n = 40$. *Bot. Jahrb.* 93: 530–538. 1973. [Comparison of the natural and synthetic hybrids between *S. asperum* and *S. officinale*.]
- & ———. Cytotaxonomic studies in the genus *Symphytum*, VII. Some hybrids between *Symphytum asperum* Lepech. and *S. officinale* in Denmark. *Proc. Nederl. Akad. Wet. C.* 78: 182–188. 1975. [Hybrids have five cytotypes resulting from backcrossing to parental species.]
- & ———. Cytotaxonomic studies in the genus *Symphytum*, VIII. Chromosome numbers and classification of ten European species. *Ibid.* 81: 162–172. 1978. [Base numbers, cytological notes on 16 taxa, new chromosome counts.]
- & ———. Population variability, hybridization and introgression in *Symphytum officinale* L. in the Netherlands. *Bot. Jahrb.* 104: 519–536. 1984. [Intraspecific hybridization between the cytotypes $2n = 40$ and $2n = 48$ in 16 populations.]
- , ——— & H. J. HUIZING. Cyto- and chemotaxonomic studies on the sections *Officinalia* and *Coerulea* of the genus *Symphytum*. *Bot. Helv.* 93: 169–192. 1983. [*S. asperum*, *S. officinale*, *S. peregrinum*, *S. ×uplandicum*; comparative morphology, chromosome numbers, pyrrolizidine alkaloids, phytosterols, triterpenoids.]
- , ——— & F. H. PERRING. Cytotaxonomic studies in the genus *Symphytum*, VI. Some notes on *Symphytum* in Britain. *Acta Bot. Neerl.* 23: 433–437. 1974. [*S. officinale*, *S. ×uplandicum*; chromosome numbers.]
- GOLDMAN, R. S., P. C. D. DEFREITAS, & S. OGA. Wound healing and analgesic effect of crude extracts of *Symphytum officinale* in rats. *Fitoterapia* 56: 323–330. 1986.*
- GRAU, J. Cytologische Untersuchungen an Boraginaceen I. *Mitt. Bot. Staatssam. München* 7: 277–294. 1968. [*Symphytum*, 290–292; *S. asperum*, $2n = 32$; *S. tuberosum*, $2n = 96$, 144.]
- . Cytologische Untersuchungen an Boraginaceen II. *Ibid.* 9: 177–194. 1971. [*Symphytum*, 185–191.]
- GVINIASHVILI, T. N. Species nova generis *Symphytum* L. ex Armenia. (In Russian.) *Notul. Syst. Geogr. Inst. Bot. Tbilis.* 26: 73–75. 1967. [*S. hajastanum*, sp. nov.]

- . De speciebus caucasicis nonnullis generis *Symphytum* L. (Sect. *Lingulata* Pawl.) nota critica. (In Russian.) *Ibid.* **27**: 87–95. 1969. [Distinguishing characters, distributions, chromosome numbers, pollen.]
- . Some data on the karyology of Caucasian species of *Symphytum* L. with respect to their taxonomy. (In Russian.) *Bot. Zhur.* **57**: 1120–1126. 1972a. [Chromosome counts for 17 species in seven sections.]
- . Species nova generis *Symphytum* L. e caucaso boreali-occidentale. (In Russian.) *Notul. Syst. Geogr. Inst. Bot. Tbilis.* **29**: 55–60. 1972b. [*S. ciscaucasicum*, sp. nov.; chromosome number, pollen, comparison with three related species.]
- . Kavkazkie predstaviteli roda *Symphytum* L. 146 pp. Tbilisi. 1976.*
- HARMATA, K. Pollen morphology and taxonomy of the genera *Symphytum* and *Procopiana*. *Prace Bot. Kraków* **5**: 6–28. 1977.*
- . A supplement of pollen morphology and taxonomy of the genera *Symphytum* and *Procopiana*. *Ibid.* **8**: 7–10. 1981.*
- HILLS, L. D. Russian comfrey—food for thought. *World Crops* **7**: 313–316. 1955. [*S. asperum* × *S. officinale*, yield, growth, and value.]
- . Comfrey report. The story of the world's fastest protein builder and herbal healer. ed. 2. viii + 98 + 41 pp. Pauma Valley, California. 1975. [*S. officinale*; uses for food, fodder, drinks, and medicine.]
- . Comfrey: fodder, food, & remedy. 253 pp. New York. 1976. [*S. officinale*; uses and economic values; appendices by various authors on importance in medicine, alkaloid content, chemical constitution of allantoin.]
- . Notes on the genus *Symphytum*. *Garden London* **108**: 215. 1983.*
- HIRONO, I., H. MORI, & M. HAGA. Carcinogenic activity of *Symphytum officinale*. *Jour. Natl. Cancer Inst.* **61**: 865–869. 1978. [Rats fed diet containing leaves of *S. officinale* developed cancer.]
- HUIZING, H. J., T. W. J. GADELLA, & E. KLIPHUIS. Chemotaxonomical investigations of the *Symphytum officinale* polyploid complex and *S. asperum* (Boraginaceae): the pyrrolizidine alkaloids. *Pl. Syst. Evol.* **140**: 279–292. 1982. [Interspecific hybrids contain the pyrrolizidine complement of both parental species.]
- , T. M. MALINGRÉ, T. W. J. GADELLA, & E. KLIPHUIS. Chemotaxonomical investigations of the *Symphytum officinale* polyploid complex and *S. asperum* (Boraginaceae): phytosterols and triterpenoids. *Pl. Syst. Evol.* **143**: 285–292. 1983. [Phytosterols have no chemotaxonomic value, but triterpenoids provided evidence for the hybrid origin of *S. ×uplandicum* from *S. asperum* and *S. officinale*.]
- HYDE, P. W. Comfrey. *Herbarist* **40**: 37–39. 1974. [*S. officinale*.]
- INGRAM, J. Studies in the cultivated Boraginaceae. 5. *Symphytum*. *Baileya* **9**: 92–99. 1961. [Seven taxa, key, illustrations, descriptions.]
- JAARSMA, T. A., E. LOHMANN, T. W. J. GADELLA, & T. M. MALINGRÉ. Chemotaxonomy of the *Symphytum officinale* agg. (Boraginaceae). *Pl. Syst. Evol.* **167**: 113–127. 1989. [Pyrrolizidine alkaloids and triterpenes analyzed from tiny leaf fragments of herbarium material of *S. officinale*, including *S. bohemicum* and *S. tanaicense*.]
- KADANS, J. M. Modern encyclopedia of herbs. 256 pp. New York. 1970. [Comfrey (*S. officinale*), 97–103.]
- KRAHULCOVÁ, A. Selected chromosome counts of the Czechoslovak flora I. *Folia Geobot. Phytotax.* **23**: 375–381. 1988. [*S. officinale*, 380.]
- KURTTO, A. Taxonomical status of *Symphytum floribundum* and *S. ×Ferrariense* (Boraginaceae). *Ann. Bot. Fenn.* **18**: 13–21. 1981. [Interspecific hybridization, taxonomy, nomenclature.]
- . Taxonomy of the *Symphytum asperum* aggregate (Boraginaceae), especially in Turkey. *Ibid.* **19**: 177–192. 1982. [Taxonomy and distribution of six taxa; new taxa, new combinations.]

- . Taxonomy of *Symphytum ottomanum*, *S. pseudobulbosum*, and *S. orientale* (Boraginaceae). *Ibid.* **22**: 319–331. 1985. [Morphology, palynology, and ecology support the hybrid origin of *S. pseudobulbosum* from the other two species; lectotypifications.]
- KUSNETSOV, N. Caucasian species of the genus *Symphytum* (Tourn.) L. (In Russian.) *Mém. Acad. Imp. Sci. St. Pétersbourg, Ser. 8, Phys. Math.* **25**: 1–94. 1910.*
- LESLIE, A. C. A new alien *Symphytum*. *B.S.B.I. News* **30**: 16, 17. 1982. [*S. grandiflora* naturalized in England.]
- LINDMAN, C. A. M. Über *Symphytum orientale* L. und *Symphytum uplandicum* Nym. *Bot. Not.* **1911**: 74–77. 1911.
- MACBRIDE, J. F. The correct name of an introduced *Symphytum*. *Rhodora* **18**: 23–25. 1916. [*S. asperum*; see GADELLA, 1984.]
- MAMCHUR, F. I., S. O. BAKIN, & B. M. ZUZUK. Comfrey (*Symphytum officinale*) as a medicinal plant. *Farm. Zhur. Kiev* **1986**(1): 30–33. 1986.*
- MATHIEU, R. F. Quaker or Russian comfrey. *Herbarist* **44**: 16–25. 1978. [*S. ×uplandicum*; history, economic importance, cultivation.]
- MATTOCKS, A. R. Toxic pyrrolizidine alkaloids in comfrey. *Lancet* **1980**(2): 1136, 1137. 1980. [Alkaloid contents of *S. ×uplandicum*, toxicity.]
- MEDVEDEV, P. F. Species of *Symphytum* L. used as forage plants. (In Russian.) *Rastit. Resur.* **7**: 49–55. 1971.*
- MEKKI, L., H. HART, N. Z. EL-ALFY, A. DEWEDAR, & T. W. J. GADELLA. The Giemsa C-banded karyotype of diploid *Symphytum officinale* (Boraginaceae). *Acta Bot. Neerl.* **36**: 33–37. 1987. [All chromosomes can be distinguished morphologically on the basis of banding, relative length, and position of centromere; variation in satellite numbers.]
- MURÍN, A., & J. MÁJOVSKÝ. Die Bedeutung der Polyploidie in der Entwicklung der in der Slowakei wachsenden Arten der Gattung *Symphytum* L. *Acta Fac. Rer. Nat. Univ. Comen. Bot.* **29**: 1–25. 1982. [*S. angustifolium*, *S. cordatum*, *S. officinale*, *S. tuberosum*; chromosome numbers, polyploidy.]
- PADUA, L. S. DE. Anatomy of *Symphytum officinale* L. Philipp. *Jour. Sci.* **107**: 41–50. 1980. [Root, petiole, and leaf-blade anatomy; trichome types.]
- PARNELL, J. *Symphytum asperum* Lepechin—a new Irish species. *Irish Nat. Jour.* **21**: 498–499. 1985. [*S. asperum*, *S. officinale*, *S. ×uplandicum*; distinguishing characters.]
- PAWLOWSKI, B. Observationes ad genus *Symphytum* L. pertinentes. (Text in Latin.) *Fragm. Flor. Geobot.* **7**: 327–356. 1961. [Infrageneric classification, interspecific hybridization, distribution in Poland of certain species complexes; new series.]
- . *Symphyta mediterranea nova vel minus cognita*. (Text in Latin.) *Ibid.* **17**: 17–37. 1971a. [Seven species (three new); taxonomy, distributions, illustrations.]
- . De genere *Procopiania* Guşuleac. (Text in Latin.) *Ibid.* 39–58. 1971b. [Three species; descriptions, distributions, illustrations, hybridization, maps.]
- . *Symphytum*. In: T. G. TUTIN, et al., eds., *Fl. Europaea* **3**: 103–105. 1972. [Fourteen species; *Procopiania* (three species) recognized as distinct from *Symphytum*.]
- PERRING, F. H. *Symphytum*. Pp. 535–355 in C. A. STACE, ed., *Hybridization and the flora of the British Isles*. London, New York, and San Francisco. 1975a. [*S. asperum*, *S. officinale*, *S. tuberosum*.]
- . *Symphytum* survey. *Watsonia* **10**: 296, 297. 1975b. [Chromosome numbers, distinguishing characters, and descriptions of *S. asperum*, *S. officinale*, and *S. ×uplandicum*.]
- PITOT, A. Isolement et chute, à maturité, de l'akène de *Symphytum orientale* L. *Bull. Soc. Bot. France* **83**: 496–500. 1936. [Fruit anatomy.]
- . L'ovaire du *Symphytum orientale* L. *Ibid.* **84**: 393–400. 1937. [Anatomy of developing ovary.]

- PLASKETT, L. G. Preparation of protein concentrates from *Symphytum asperum*, Russian comfrey, for nonruminant feed and human foods. *Food Chem.* 7: 109-116. 1981.*
- PUGSLEY, H. W. The forms of *Symphytum tuberosum* L. *Jour. Bot. London* 69: 89-97. 1931.
- ROITMAN, J. Comfrey and liver damage. *Lancet* 1981(1): 944. 1981. [*S. asperum*; pyrrolizidine alkaloid contents; toxic effects.]
- RUNEMARK, H. Studies in the Aegean flora. XI. *Procopiana* (Boraginaceae) included into *Symphytum*. *Bot. Not.* 120: 84-94. 1967. [Morphology, palynology, and cytology support the reduction of *Procopiana* to synonymy of *Symphytum*; *S. circinale*, sp. nov.; new combinations.]
- SEIDENBINDER, M., & R. VERLAQUE. In: Chromosome number reports LXXXVI. *Taxon* 34: 159-164. 1984. [*S. tuberosum*, 161, 2n = ca. 128.]
- SENAY, P. *Symphytum peregrinum* Ledeb. et ses hybrides avec *S. officinale* L. *Bull. Soc. Bot. France* 87: 313-322. 1940.
- SHIRATO, K., T. SHINTANI, G. NAKANISHI, A. KAMIZYO. Chromosome numbers in genus *Symphytum*. *Chromosome Inf. Serv.* 38: 21-23. 1985. [*S. asperum*, *S. officinale*, *S. peregrinum*.]
- SOUÈGES, R. Embryogénie des Boragacées. Développement de l'embryon chez le *Symphytum officinale* L. *Compt. Rend. Acad. Sci. Paris* 212: 245, 246. 1941.
- STEARNS, W. T. The Greek species of *Symphytum* (Boraginaceae). *Ann. Mus. Goulandris* 7: 175-220. 1986. [Five species; descriptions, distributions, illustrations, maps; translation from Russian of GVINIASHVILI'S (1976) key to the Caucasian species.]
- TUTIN, T. G. The genus *Symphytum* in Britain. *Watsonia* 3: 280, 281. 1956. [Two native species, five naturalized, and one interspecific hybrid.]
- ULUBELEN, A., & S. BOĞANCA. Anadoline, a new *Senecio* alkaloid from *Symphytum orientale*. *Tetrahedron Lett.* 1970: 2583-2585. 1970.
- & ———. Alkaloidal and other constituents of *Symphytum orientale*. *Phytochemistry* 10: 441, 442. 1971. [Identification of four pyrrolizidine alkaloids.]
- & F. ÖCAL. Alkaloids and other compounds of *Symphytum tuberosum*. *Phytochemistry* 16: 499, 500. 1977. [Pyrrolizidine alkaloids, sugars, amino acids, steroidal alcohols, hydrocarbons.]
- VAN LOON, J. C., & J. J. H. M. OUDEMANS. In: IOPB chromosome number reports LXXXV. *Taxon* 31: 342-368. 1982. [*S. ottomanum*, 2n = 20; *S. tuberosum* subsp. *nodosum*, 2n = 64; 344.]
- WADE, A. E. The history of *Symphytum asperum* Lepech. and *S. xuplandicum* Nyman in Britain. *Watsonia* 4: 117, 118. 1958.
- WANG, G.-L., Z.-S. LI, & Q.-X. MENG. An observation of chromosome numbers of comfrey from different sources. (In Chinese; English summary.) *Acta Phytotax. Sinica* 21: 55-59. 1983. [*S. peregrinum*, 2n = 40.]
- WCISLO, H. Karyological studies in *Symphytum* L. *Acta Biol. Cracov. Bot.* 15: 153-163. pl. 36. 1972. [*S. cordatum*, *S. officinale*, *S. tuberosum*; chromosome numbers of Polish populations.]
- WICKENS, G. E. A revision of *Symphytum* L. in Turkey and adjacent areas. *Notes Bot. Gard. Edinburgh* 29: 157-180. 1969. [Twenty-nine species; descriptions, distributions, key, sectional classification, new taxa.]
- . *Symphytum*. In: P. H. DAVIS, ed., *Fl. Turkey* 6: 378-386. 1978. [Twenty species recognized; *Procopiana* reduced to synonymy of *Symphytum*.]
- WILKES, M. Comfrey—the cinderella of plants. *Herbarist* 33: 47-50. 1967. [Values as food and fodder; medicinal and nutritional properties.]

Tribe 6. MYOSOTIDEAE Reichenb., Icon. Fl. Germ.

18: 70. 1857.

18. *Myosotis* Linnaeus, Sp. Pl. 1: 131. 1753; Gen. Pl. ed. 5. 63. 1754.

Annual or perennial herbs, usually softly pubescent. Leaves entire, alternate, the lower ones petiolate, the upper sessile. Cymes scorpioid or raceme-like [rarely 1 flowered], ebracteate [or bracteate]. Calyx divided beyond the middle into lanceolate or deltoid lobes, persistent, somewhat accrescent in fruit, symmetrical or asymmetrical, pubescent with straight and/or uncinuate trichomes. Corolla white, blue [brown or yellow], rotate, salverform [campanulate or funnelform]; lobes spreading, rounded, contorted in bud; faucal scales 5, opposite the corolla lobes, papillose, white or yellow. Stamens epipetalous, included [or long exserted]; anthers oblong to ovate, nearly equaling [or much shorter than] filaments, appendaged at apex. Ovary lobes glabrous; style filiform, included [or exserted]; stigma entire or 2 lobed. Nutlets 4, occasionally fewer by abortion, erect, ovoid to ellipsoid, somewhat compressed, smooth and glossy, whitish to brown or black, with a distinct rim, laterally compressed, attachment scar basal, usually small, without [or sometimes with] a spongy strophiolate appendage; gynobase convex or flat. Base chromosome numbers 7–12. (Including *Echioides* Moench, non Fabricius, non Gómez Ortega; *Exarrhena* R. Br.; *Scorpiurus* Haller, non L., non Le Jolis; *Strophlostoma* Turcz.) LECTOTYPE SPECIES: *M. scorpioides* L.; see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. 3: 85. 1913. (Name from Greek *myos*, of a mouse, and *ous*, ear, from the soft and short leaves of some species; see Fernald, family refr.) — FORGET-ME-NOT, MOUSE EAR, SCORPION GRASS.

A well-defined but taxonomically difficult genus of about 100 species distributed primarily in the temperate areas of both hemispheres, or in the high mountains of the tropics. The majority of species (about 60) are distributed in Europe and/or Asia, and the ranges of some extend into North America or northern Africa. The greatest concentration of species within a given area is in New Zealand, where about 35 are endemic. *Myosotis* is poorly developed elsewhere; two species are restricted to North America, one to South America, and three to Africa. The genus is represented in the southeastern United States by eight species, of which three are indigenous.

The infrageneric classification of *Myosotis* is controversial, and there is a lack of agreement among various treatments, particularly in the limits, rank, and number of subdivisions. De Cañdolle recognized 41 species, of which 28 were assigned to four sections (sects. *Eumyosotis*, *Exarrhena* (R. Br.) A. DC., *Strophlostoma* (Turcz.) Endl., and *Gymnomyosotis* A. DC.) and 13 were unassigned. He relied heavily on the nature of the faucal appendages of the corolla and on whether the anthers are exserted or included. Stroh (1941), who accepted all but the last section, recognized 104 species in the genus and distributed

those of New Zealand in sects. *Exarrhena* and *Myosotis*. The latter section included 87 species.

Popov (1953) placed the 25 species that grow in the Soviet Union in two subgenera, four series, and four subseries. His account, which was followed by Riedl (1967), was based on characters of questionable value. He relied heavily on features such as habit, type of trichomes on the fruiting calyx (hooked vs. straight and appressed), and presence vs. absence of a caruncle on the seeds.

On the basis of pollen morphology, nature of the stigmatic lobes and papillae, and type of faucal appendages, Grau & Schwab divided *Myosotis* into two well-marked sections. Section MYOSOTIS, which included all the Eurasian, African, and North American species, except the *M. discolor* group, has very small pollen grains that are constricted at the equatorial region, finely perforate at the poles, and lacking any sculpture. It also has somewhat 2-lobed stigmas that have slightly differentiated, very small papillae. Section EXARRHENA included all of the species of New Zealand and Australia, as well as the *M. discolor* group and the Patagonian *M. albiflora* Banks & Solander. Members of this section have pollen grains lacking polar perforations but with a conspicuously sculptured exine, as well as entire stigmas with large, clavate papillae. Except for *M. discolor*, which belongs to sect. EXARRHENA, all other species that grow in the Southeastern States belong to sect. MYOSOTIS.

Myosotis is readily distinguished from all genera of the subfamily Boraginoideae in having contorted instead of imbricate aestivation of the corolla. The glossy, ovoid to ellipsoid nutlets and faucal appendages of the corolla throat separate the genus from other members of the family that grow in the Southeast.

Myosotis verna Nutt. (*M. inflexa* Engelm.; *M. virginica* (L.) BSP. *sensu* authors, not as to type), scorpion grass, grows on dry to moist soil in woodlands, fallow and cultivated fields, river bottoms, prairies, pine bluffs, and scrub oak barrens, as well as along stream banks and roadsides. It is native to and widespread in Canada and the United States and has been reported from all of the Southeastern States. Fernald (1941), Johnston *et al.*, Rickett, Small (1933) (as *M. virginica*), and Steyermark have all recorded *M. verna* from Florida, but Ward & Fantz concluded that it has not been collected there. I have not seen any material from Florida. Jones & Coile have mapped it in seven counties in Georgia. It also occurs in Lee County (Godfrey 58444, GH).

Myosotis macrosperma Engelm. (*M. verna* Nutt. var. *macrosperma* (Engelm.) Chapman, *M. virginica* (L.) BSP. var. *macrosperma* (Engelm.) Fern.), also indigenous, grows on moist to wet, loamy to sandy, somewhat calcareous soils, particularly along stream bottoms, in fields, woodlands, floodplain forests, and on bluffs. It is distributed in the eastern and central United States, including perhaps all of the Southeastern States. Jones & Coile mapped it in nine counties in Georgia, to which Clay County can be added (Thorne & Muenscher 7834,

GH). The species has been reported to be indigenous in Argentina (Johnston, 1925b, 1927).

Myosotis macrosperma and *M. verna* differ from the other species of the Southeast in having white corollas and asymmetric calyces with unequal lobes. The former is readily distinguished from the latter by its large (3–10 mm), deciduous fruiting calyces that are usually more than 1 cm apart on the rachis. In contrast *M. verna* has smaller (3–5.5 mm), persistent fruiting calyces that are less than 1 cm apart on the rachis. Therefore, the infructescence of *M. verna* is denser than that of *M. macrosperma*.

Both Steyermark and E. B. Smith (1978, 1988) recognized *Myosotis macrosperma* as a variety of the earlier published *M. verna*. In my opinion, both plants are distinct species, and Steyermark's reasoning for maintaining them at the varietal rank is unjustified. The two species are very common in Arkansas, and I have not seen any material from there or from elsewhere in North America that would suggest interspecific hybridization or would cast doubt on the reliability of the distinguishing features of these two species.

The third indigenous North American species is *Myosotis laxa* Lehm. It is represented in this continent by subsp. *laxa*, in Europe by subsp. *baltica* (Samuels.) Hylander ex Nordh. and subsp. *caespitosa* (C. F. Schultz) Hylander ex Nordh., and in Asia by subsp. *caespitosa*. Subspecies *laxa* (*M. caespitosa* C. F. Schultz var. *laxa* (Lehm.) A. DC., *M. palustris* (L.) Lam. var. *laxa* (Lehm.) A. Gray), $2n = 84$, grows in wet ground, mud, or shallow water in bogs and along marshy shores and stream banks. It is distributed from Newfoundland west through Ontario and Minnesota into British Columbia, south into California, and east into North Carolina and Tennessee. Several authors (e.g., Duncan & Kartesz, Fassett, Fernald (family refr.), Gleason, Godfrey & Wooten, Rickett, and Small (1933)), have reported *M. laxa* from Georgia, but Jones & Coile did not map it as occurring there. The species is readily distinguished by its regular fruiting calyx (bearing straight, appressed trichomes); decumbent, nonstoloniferous stems; corollas 2–5 mm broad; and styles shorter than the nutlets. It has been reported from Chile and Argentina (Johnston, 1927), where it is believed to be introduced.

The five remaining species of *Myosotis* that grow in the southeastern United States are all naturalized European weeds. *Myosotis scorpioides* L. (*M. scorpioides* var. *palustris* L., *M. scorpioides* subsp. *palustris* (L.) F. Herm., *M. palustris* (L.) Lam.), forget-me-not, $2n = 22, 44, 66$, is naturalized in Canada and various parts of the United States, including western North Carolina, Tennessee, Alabama, and Louisiana. Fassett, Fernald (family refr.), Johnston (1924a), Rickett, Small (1933), and Steyermark reported it from Georgia, but Jones & Coile did not include it in their account.

Linnaeus (Sp. Pl. 1: 131. 1753) recognized two varieties (vars. *arvensis* and *palustris*) under *Myosotis scorpioides*. These are now regarded as species, following Hill's treatment (Veg. Syst. 7: 55. 1764),

in which var. *arvensis* was raised to specific rank and var. *palustris* was treated as *M. scorpioides*.

Myosotis scorpioides resembles *M. lara* in various aspects of the fruiting calyx, but is easily distinguished by its broader corollas 5–10 mm wide, longer styles nearly equal to or exceeding the nutlets, and creeping stems that are stoloniferous at the base. It grows primarily on wet soil in meadows and wooded areas, as well as along stream banks and on marshy shores. It is commonly cultivated as an ornamental garden plant and is a sporadic escape.

Myosotis scorpioides is highly variable, and Wade (1930) recognized as many as 14 varieties and eight forms. Winsor suggested that the populations of this species in Michigan, Ohio, and Pennsylvania represent several Eurasian varieties, but he did not specify which of these have become naturalized in these states.

Myosotis arvensis (L.) Hill (*M. scorpioides* var. *arvensis* L.; see Grau (1968) for 15 additional synonyms), garden forget-me-not, $2n = 36, 48, 52, 66$, is sporadically naturalized in Canada and the United States and has been reported in our area from North Carolina (Hommersand; Small, 1933). It has a regular fruiting calyx (bearing hooked trichomes), fruiting pedicels longer than the calyx, and a blue corolla limb only 2–4 mm broad. The related *M. sylvatica* Hoffm., the garden forget-me-not, $2n = 14, 18, 20, 22, 24, 32$, has been reported as an escape from cultivation in North Carolina (Hommersand) and is sporadically naturalized elsewhere in North America. It resembles *M. arvensis* in the characters above except that it has a wider (5–8 mm) corolla limb and is a biennial or perennial, instead of an annual.

Myosotis discolor Pers. (*M. versicolor* (Pers.) Sm., *M. arvensis* (L.) Hill subsp. *versicolor* Pers.; see Grau (1968) for 13 additional synonyms), $2n = 64, 72$, is sporadically naturalized in Canada and the United States and has been reported in the Southeastern States from Alabama (Godfrey & Wooten), Durham, Granville, Orange, and Stokes counties, North Carolina (Hommersand), and from Jasper County, Georgia (Jones & Coile).

The remaining species naturalized in the Southeast, *Myosotis stricta* Link ex Roemer & Schultes (*M. collina* Hoffm., *M. micrantha* of authors, non Pallas ex Lehm., non Guss.), $2n = 24, 36, 48$, is a Eurasian plant well established as a weed in southern Canada and the northern United States. It has been reported (as *M. micrantha* Pallas ex Lehm.) in North Carolina from Durham and Haywood counties (Hommersand) and Mecklenburg County (Mellichamp *et al.*), and in Arkansas from Crittenden County (Wilcox). However, E. B. Smith (1978) excluded it from Arkansas, mainly on the basis of its distribution as given in Fernald (family refr.). The record needs verification, but it is likely that this weedy species will be reported from elsewhere in the Southeastern States.

Most North American authors, including Cronquist (1984), Gleason, Hommersand, and Johnston (1924a), have reduced *Myosotis stricta* to synonymy under *M. micrantha* Pallas ex Lehm., which was described

from southern Russia. I have not seen the original publication of *M. micrantha*, but on the basis of De Candolle's brief description it, the plant should be excluded from *Myosotis*, since it has axillary, subsessile, yellow flowers and rugose nutlets.

Myosotis stricta is closely related to *M. discolor*, which it resembles in having a regular fruiting calyx with hooked trichomes and fruiting pedicels shorter than the mature calyx. *Myosotis stricta* is easily distinguished by being floriferous to near the base, including axils of lower leaves, and having hooked trichomes on the lower leaf surface, especially on veins, bright to pale blue corollas, and styles shorter than the nutlets. In contrast *M. discolor* is floriferous only above the leaves and has straight trichomes on the lower leaf surface, pale yellow flowers that become blue, and styles nearly equal to or longer than the nutlets. The length of the corolla relative to that of the calyx, as given by Johnston (1924a) and Hommersand, is unreliable for distinguishing between the two species.

The tribal placement of *Myosotis* has been controversial, for it has several features that are anomalous in tribes Boragineae, Lithospermeae, and Eritrichieae, in each of which it has been placed previously. It resembles the Boragineae in the occasional presence of strophiolate nutlets but differs markedly in the aestivation of the petals and in lacking the basal annular rim on the nutlets. Johnston (1924b) placed *Myosotis* in the Eritrichieae on the basis of its solitary stigma, blue flowers, and somewhat compressed nutlets. However, the presence in *Myosotis* of contorted corolla lobes, a flat gynobase, and nutlets without keels make it anomalous in that tribe. The placement of *Myosotis* in a unigeneric tribe is most appropriate, and this disposition has been supported by the majority of recent students of the Boraginaceae.

According to Knuth, Macleod observed gynodioecism in *Myosotis scorpioides* (as *M. palustris*) and Kerner von Marilaun reported heterostyly in other species. However, these observations need verification. Recent students of the genus have given no indication that the two reproductive systems are present.

The flowers of *Myosotis discolor* are bright yellow at anthesis, and they change through red to blue. The style is exerted at anthesis, but as the flower becomes older the corolla tube elongates and the stigma contacts the anthers, thus enforcing self-pollination (Knuth).

Varoupeoulos reported that self-incompatibility in *Myosotis scorpioides* is controlled by a polygenic system. Seed set resulting from self-pollination varies from zero to 95 percent. Complete self-incompatibility results from homozygosity at more than a certain critical number of gene loci, and the degree of self-compatibility is positively correlated with heterozygosity. The extent of protandry was observed to correlate with selection for self-incompatibility. She also noted that in *M. scorpioides* the occurrence of trinucleate pollen would suggest a sporophytic system of incompatibility, whereas the site of inhibition of the pollen tube indicates a gametophytic system.

Chromosome numbers have been reported for about 60 species of *Myosotis*. Although a continuous series of base numbers from seven to twelve is known, the majority of species are based on $n = 11$ or 12. In fact Grau (1975) emphasized (p. 83) that $n = 12$ "must be without any doubt the primary base number of this genus." Polyploidy probably has played an important role in the evolution of the genus, as evidenced by its occurrence in more than 50 percent of the species studied. Polyploidization and structural rearrangements followed by loss of chromosomes were suggested by Przywara (1983a, b) as important factors in chromosomal evolution in *Myosotis*.

The karyotypes of several species of *Myosotis* have been analyzed, and Grau (1975) suggested that two chromosome types, metacentric and acrocentric, can be distinguished in the European species. She was even successful in distinguishing between the three subspecies of *M. sylvatica* on the basis of their karyotypes and chromosome numbers.

Natural hybridization has been documented between *Myosotis scorpioides* and *M. laxa* subsp. *caespitosa* (as *M. caespitosa* C. F. Schultz) (Benoist, 1958, 1975). The hybrid, *M. × Suzae* Domin, is a vigorous, partially fertile perennial that is morphologically intermediate between the parental species and that occasionally forms complex populations. It produces partially sterile pollen of highly variable shape and size. It has been found in Britain, Czechoslovakia, and Germany, but Schuster (1967) questioned its existence. Putative hybridization in Czechoslovakia has also been reported between *M. sylvatica* and each of *M. alpestris* Schmidt, *M. scorpioides*, *M. ramosissima* Rochel, and *M. arvensis*, and between the last and both *M. alpestris* and *M. ramosissima*. Hybridization in the Netherlands between *M. laxa* subsp. *caespitosa* ($2n = 88$) and *M. nemorosa* Besser (as *M. palustris* subsp. *nemorosa*) ($2n = 22$), has been documented by Berg & Kaastra; the hybrid was found to have $2n = 55$. Hybridization between some other pairs of species has been reported, but most reports lack supportive experimental evidence and need confirmation.

Leaf fatty acids have been analyzed for *Myosotis alpestris*, *M. arvensis*, *M. scorpioides*, *M. stricta*, and *M. sylvatica* (Jamieson & Reid; Tétényi). Their profiles show differences in the content of linoleic and linolenic acids that may have chemotaxonomic value. Pyrrolizidine alkaloids have been surveyed in a few species, including *M. scorpioides* and *M. sylvatica* (Resch *et al.*; Smith & Culvenor). However, the data on both fatty acids and alkaloids are too scanty for meaningful conclusions to be drawn.

Nutlet dispersal in *Myosotis* is poorly studied. Species that produce an elaiosome (strophiole) at the base of the nutlet are believed to be dispersed by ants (Bresinsky). Ridley suggested that plants of *M. arvensis* are eaten by roe deer (*Capreolus capreolus*), and plants have been found growing from the scat of these animals. He also observed that in *M. arvensis*, *M. discolor* (as *M. versicolor*), and *M. stricta* (as *M. collina*), all of which have fruiting calyces with hooked trichomes, dispersal is by small mammals, particularly rabbits. The

fruiting calyces cling to animal fur (and to human clothing) and are detached from the fruiting pedicels. Steyermark indicated that birds feed on the nutlets of various species of *Myosotis*, but it is not known whether the seeds retain viability after passing through the digestive tract.

Myosotis scorpioides and *M. sylvatica* are widely cultivated ornamentals. The former is often planted in wet areas, around pools, and along streams, whereas the latter is mostly grown in gardens. A few medicinal uses have been attributed to *Myosotis* (Uphof), and a few species are widely distributed weeds.

REFERENCES:

- Under family references see AHN & LEE; BACIU; BAILEY *et al.*; BAILLON; BENTHAM & HOOKER; BOLKHOVSKIKH *et al.*; BREWBAKER; BRITTON; BRITTON & BROWN; BULL *et al.*; DE CANDOLLE; CHAPMAN; G. C. S. CLARKE; CLEWELL; CORRELL & CORRELL (1972); CORRELL & JOHNSTON; DíEZ (1984); DUNCAN & KARTESZ; FABRE; FERNALD; GATTINGER; GLEASON; GODFREY & WOOTEN; GOLDBLATT (1981, 1984, 1985, 1988); GUNN *et al.*; HEGI; HOFMANN *et al.*; HOMMERSAND; ISHIKURA; JAMIESON & REID; JODIN; JOHNSTON (1924a, b, 1925b, 1927); JOHNSTON *et al.*; JONES & COILE; KERNER VON MARILAU; KLEIMAN *et al.*; KNUTH; LUBBOCK; MACROBERTS; MARTICORENA; MITCHELL & ROOK; MOHR; R. J. MOORE (1973, 1974, 1977); MÜLLER; ORNDUFF (1967, 1968, 1969); POLLARD & AMUTI; POPOV (1953); RICKETT; RIDLEY; RIEDL (1967); SAHAY; SCHAEFER; SIEBERT; SHARP *et al.*; SINGH; SMALL (1903, 1933); E. B. SMITH (1978, 1988); L. B. SMITH; STEYERMARK; SYNGE; TÉTÉNYI; TOELKEN; UPHOF; WARD & FANTZ; WILLAMAN & LI; and WOFFORD.
- ALLEN, D. E. *Myosotis discolor* Pers. Proc. Bot. Soc. Brit. Is. 6: 49, 50. 1965. [Notes on distribution in the British Isles.]
- APELGREN, K. Some problematic species of *Myosotis* in the Baltic region. (In Swedish; English summary.) Sv. Bot. Tidskr. 80: 145–150. 1986. [*M. baltica*, *M. caespitosa*, *M. praecox*, *M. scorpioides*; variation, distribution, distinguishing characters.]
- BEAL, E. O. A manual of marsh and aquatic vascular plants of North Carolina. N. Carolina Agr. Exper. Sta. Tech. Bull. 247. iv + 298 pp. 1977. [*M. laxa*, *M. scorpioides* (as *scirpoides*), 239.]
- BECKETT, K. New Zealand forget-me-nots. Garden London 106: 257–259. 1981.*
- BÉGUINOT, A. Materiali per una monografia del genere *Myosotis* L. Ann. Bot. Roma 1: 275–295. 1904. [Twelve species in two sections.]
- BENOIT, P. M. *Myosotis caespitosa* × *scorpioides*. Proc. Bot. Soc. Brit. Is. 3: 46, 47. 1958.
- . *Myosotis*. Pp. 356, 357 in C. A. STACE, ed., Hybridization and the flora of the British Isles. London, New York, and San Francisco. 1975. [Seven interspecific hybrids involving six species.]
- BERG, C. C., & R. C. KAASTRA. *Myosotis palustris* en *M. laxa* in Nederland. (English summary.) Gorteria 6: 141–150. 1973. [Three subspecies recognized; distribution, maps, key, chromosome numbers, putative interspecific hybridization.]
- BERNARD, F. G. Forme blanche de *Myosotis arvensis* (L.) Hill (Boraginaceae). Nat. Canad. 95: 801, 802. 1968. [The new forma *albiflorum* described.]
- BEUZENBERG, E. J., & J. B. HAIR. Contributions to a chromosome atlas of the New Zealand flora—25. Miscellaneous species. New Zealand Jour. Bot. 21: 13–20. 1983. [Counts for eight species, 13, figs. 21–24.]

- BLAISE, S. Observations on the karyosystematics and ecology of *Myosotis sylvatica* (Ehrh.) Hoff. *sensu latissimo*. (In French.) *Compt. Rend. Acad. Sci. Paris* **260**: 647-650. *map.* 1965.*
- . Caryologie et morphologie comparée de *Myosotis stricta* Link et de *Myosotis ruscinnonensis* Rouy. *Ibid.* **262**: 103-106. 1966. [Chromosome numbers, distinguishing characters.]
- . Considérations biosystématiques sur le groupe *Myosotis* "discolor." *Ibid.* **268**: 2682-2685. 1969a. [The putative allopolyploid origin of *M. discolor* subsp. *discolor*.]
- . Les méthodes de l'analyse factorielle des correspondances appliquées à la biosystématique de quelques espèces de *Myosotis* L. *Compt. Rend. Soc. Biol.* **163**: 83-86. 1969b. [*M. ramosissima*.]
- . Biosystématique de *Myosotis congesta* Shuttleworth ex Albert et Reynier. *Compt. Rend. Acad. Sci. Paris* **270**: 502-505. 1970. [Chromosome numbers, palynology, nomenclature.]
- . Problèmes taxinomiques posés par l'homogénéité apparente du genre *Myosotis*. (English summary.) *Candollea* **27**: 65-81. 1972. [Use of cytological and palynological data in the separation of members of certain species complexes.]
- . In: Chromosome number reports LXX. *Taxon* **30**: 68-80. 1981. [Counts for 15 taxa of *Myosotis*, 76.]
- , J.-P. BRIANE, & M.-O. LEBEAUX. Le genre *Myosotis*: exemples d'application des méthodes numériques en taxinomie végétale. Pp. 326-359 in J.-P. BENZÉER *et al.*, eds., *L'analyse des données: I. La taxinomie*. 1973.*
- BRESINSKY, A. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. (English summary.) *Biblot. Bot.* **126**. 54 pp. 1963. [*Myosotis*, 21, 22.]
- BRUMMIT, R. K. *Myosotis Arnoldii*. Boraginaceae. *Bot. Mag.* **184**: 17-19. *pl.* 841. 1982. [A New Zealandic species with brown flowers and exerted stamens.]
- CHATTERS, R. M. Induction by fast neutrons of mutations in *Antirrhinum* and *Myosotis*. *Science* **88**: 241, 242. 1938. [Treatment induced variation in numbers of corolla and calyx lobes in *Myosotis*.]
- CHEVALIER, A. Les *Myosotis* du groupe *sylvatica* et *arvensis*. *Bull. Mus. Natl. Hist. Nat. Paris* II. **13**: 187-194. 1941. [Variation, interspecific hybridization.]
- ELKINGTON, T. T. Biological flora of the British Isles. *Myosotis alpestris* F. W. Schmidt. *Jour. Ecol.* **52**: 709-722. 1964.
- FASSETT, N. C. A manual of aquatic plants. Revised ed. ix + 405 pp. Madison, Wisconsin. 1957. [*M. laxa*, *M. scorpioides*, 285.]
- FAVARD, A. Ontogénèse de l'inflorescence du *Myosotis* des Alpes. Ontogénèse de l'inflorescence primaire. *Compt. Rend. Acad. Sci. Paris* **250**: 908-910. 1960a.
- . Ontogénèse de l'inflorescence du *Myosotis* des Alpes. Ontogénèse des l'inflorescences partielles de second ordre. *Ibid.* 1534-1536. 1960b.
- FERNALD, M. L. Another century of additions to the flora of Virginia. *Rhodora* **43**: 635-657. 1941. [*M. macrosperma*, *M. verna*; nomenclature, distribution, distinguishing characters, 636, 637.]
- FERNANDES, R. Notas sobre a flora de Portugal-X. *Bol. Soc. Brot.* II. **44**: 109-171. 2 pls. 1970. [*Myosotis*, 111-142; *M. secunda*, *M. stolonifera*, *M. Welwitschii*.]
- & M. T. LEITÃO. Contribution to the karyosystematic knowledge of the genus *Myosotis*. *Anal. Estac. Exp. Aula Dei* **9**: 210-222. 1969.*
- FRITSCH, K. Ueber Gynodioecie bei *Myosotis palustris* (L.). *Ber. Deutsch. Bot. Ges.* **18**: 472-480. 1900.
- GETTLER, L. Vergleichend-zytologische Untersuchungen an *Myosotis*. *Jahrb. Wiss. Bot.* **83**: 707-724. 1936.*
- GHAU, J. Die Zytotaxonomie der *Myosotis-alpestris*- und der *Myosotis-silvatica*-Gruppe in Europa. *Österr. Bot. Zeitschr.* **111**: 561-617. 1964. [Taxonomy, chromosome numbers, karyotypes, palynology, distribution, keys.]

- . Karyotypphylogenie bei *Myosotis*. Ber. Deutsch. Bot. Ges. 77(Sondernummer): 99–101. 1965a. [Base chromosome numbers and ploidy levels in species groups.]
- . Cytotaxonomische Bearbeitung der Gattung *Myosotis* L., I. Atlantische Sippen um *Myosotis secunda* A. Murr. Mitt. Bot. Staatssam. München 5: 675–688. 1965b. [*M. secunda*, *M. stolonifera*, *M. Welwitschii*; chromosome numbers, distribution, key, illustrations.]
- . Cytotaxonomische Bearbeitung der Gattung *Myosotis* L., II. *Myosotis sicula* s. l. Ibid. 6: 517–530. 1967. [*M. debilis*, *M. lusitanica*, *M. sicula*; chromosome numbers, distribution, key.]
- . Cytotaxonomische Bearbeitung der Gattung *Myosotis* L., III. Die annuellen Sippen. Ibid. 7: 17–100. 1968. [Sixteen European and Turkish species; morphology, palynology, chromosome numbers, distributions, radiation centers of species groups, taxonomy, key, illustrations.]
- . Cytotaxonomische Bearbeitung der Gattung *Myosotis* L., IV. Ergänzende Studien. Ibid. 8: 127–136. 1970. [Five species; chromosome numbers, distributions, new combinations.]
- . Studies in the genus *Myosotis*. Pp. 82–89 in S. M. WALTERS & C. J. KING, eds., European floristic and taxonomic studies. Conference Report. Farrington, Oxfordshire, England. 1975. [Value of karyotypes in the delimitation of members of the *M. alpestris*, *M. decumbens*, and *M. sylvatica* complex.]
- . *Myosotis*. In: P. H. DAVIS, ed., Fl. Turkey 6: 264–280. 1978. [Twenty-three species.]
- & P. LEINS. Pollenkorntypen und Sektionsgliederung der Gattung *Myosotis*. (English summary.) Ber. Deutsch. Bot. Ges. 81: 107–115. 1968. [Pollen morphology divides the genus into two groups.]
- & H. MERXMÜLLER. *Myosotis*. In: T. G. TUTIN, et al., eds., Fl. Europaea 3: 111–117. 1972. [Forty-one species.]
- & A. SCHWAB. Mikromerkmale der Blüte zur Gliederung der Gattung *Myosotis*. (English summary.) Mitt. Bot. Staatssam. München 18: 9–58. 1982. [Pollen, stigmas, and floral scales support the subdivision of the genus into two sections.]
- GREUTER, W., & J. GRAU. Zum vorkommen von drei Unterarten der *Myosotis refracta* Boiss. (English summary.) Candollea 25: 7–10. 1970.
- HEDBERG, I., & O. HEDBERG. Chromosome numbers of afroalpine and afromontane angiosperms. Bot. Not. 130: 1–24. 1977. [*Myosotis*, 18.]
- HOLUB, J. Bemerkungen zur Nomenclatur der in der Tschechoslowakei vorkommenden Vertreter des Komplexes *Myosotis palustris*. Preslia 38: 130–136. 1966.
- HÜLPHERS, A. *Myosotis*-studier. Sv. Bot. Tidskr. 21: 63–72. 1927. [*M. palustris*, *M. praecox*, *M. serotina*.]
- JOYAL, E. *Myosotis latifolia* and not *Myosotis sylvatica* (Boraginaceae) in California. Madroño 36: 131. 1989.
- LINDBERG, H. *Myosotis laxa* Lehm. (*M. baltica* Samuelss.). (In Finnish.) Mem. Soc. Fauna Fl. Fenn. 10: 94–96. 1933. [Distribution, notes.]
- MATTHEWS, J. F., & T. L. MELLICHAMP. Additional records to the vascular flora of the Carolinas and a selected bibliography of floristic studies, 1964–1987. Jour. Elisha Mitchell Sci. Soc. 105: 34–54. 1989. [*M. macrosperma* and *M. scorpioides* from Stanly and Cleveland counties, respectively, North Carolina, 42.]
- MELLICHAMP, T. L., J. F. MATTHEWS, & P. J. SMITHKA. New state and regional records of vascular plants in the Carolinas. Castanea 52: 95–111. 1987. [*M. micrantha* reported from Mecklenburg County, North Carolina.]
- MERXMÜLLER, H., & J. GRAU. Chromosomenzahlen aus der Gattung *Myosotis* L. Ber. Deutsch. Bot. Ges. 76: 23–29. 1963. [Twenty-five species.]

- MIZIANTY, M. Chromosome numbers of *Myosotis palustris* (L.) Nathh. in Poland. *Fragm. Flor. Geobot.* **22**: 323–330. 1976. [Three subspecies; polyploidy based on $x = 11$.]
- MOORE, L. B. Boraginaceae. In: H. H. ALLAN, *Fl. New Zealand* **1**: 806–833. 1961. [*Myosotis* represented by 34 endemic species.]
- PALACIOS-CHÁVEZ, R., & D. L. QUIROZ-GARCÍA. Catálogo palinológico para la flora de Veracruz. No. 30. Familia Boraginaceae. Género *Myosotis*. (English summary.) *Biotica* **11**: 43–46. 1986. [*M. discolor*.]
- PITILLO, J. D., & A. E. BROWN. Additions to the vascular flora of the Carolinas. III. *Jour. Elisha Mitchell Sci. Soc.* **104**: 1–18. 1988. [*M. scorpioides* in Jackson County, North Carolina, 14.]
- POPOVA, T. N. Conspectus generis *Myosotis* L. specierum Caucasicarum. *Novit. Syst. Pl. Vasc.* **13**: 219–228. 1976. [Seventeen species in two subgenera and five series; key, synonymy, distribution, notes; *M. daralaghezica*, sp. nov.]
- PRIOR, P. V. Development of the helicoid and scorpioid cymes in *Myosotis laxa* Lehm. and *Mertensia virginica* L. *Proc. Iowa Acad. Sci.* **67**: 76–81. 1960.
- PRZYWARA, L. Karyological studies in the genus *Myosotis* L. in Poland. *Acta Biol. Cracov.* **21**: 125–141. 1978. [Chromosome counts for 11 species, including *M. arvensis*, *M. discolor*, *M. scorpioides* (as *M. palustris*), and *M. sylvatica*.]
- . Karyological studies on *Myosotis sparsiflora* Mikan from Poland. *Ibid.* **25**: 79–84. 1983a. [Karyotype consists of three pairs of metacentric chromosomes and six of acrocentric, of which two pairs have satellites.]
- . Further karyological studies on the series *Palustres* M. Pop. of the genus *Myosotis* from Poland. *Ibid.* 85–102. pls. 4–6. 1983b. [*M. caespitosa*, *M. nemorosa*, *M. palustris*, *M. praecox*; karyotypes, hypothetical chromosomal constitution within series *Palustres*.]
- . Biosystematic studies on the series *Palustres* M. Pop. of the genus *Myosotis* L. from Poland. *Fragm. Fl. Geobot.* **31/32**: 77–116. 4 pls. 1986/1987. [Six species; embryology, karyology, morphology, interspecific hybridization, key to taxa.]
- RABIJS, M. Bijdrage tot de systematiek en de chorologie van *Myosotis* L. series *Palustres* M. Pop. in België. *Bull. Jard. Bot. Natl. Belg.* **42**: 403–430. 1972. [Seven species in three subseries; infraspecific taxonomy, keys, descriptions.]
- RESCH, J. F., D. F. ROSBERGER, J. MEINWALD, & J. W. APPLING. Biologically active pyrrolizidine alkaloids from the true forget-me-not, *Myosotis scorpioides*. *Jour. Nat. Prod.* **45**: 358–362. 1982. [Four pyrrolizidine alkaloids isolated and characterized; toxic effects.]
- SCHUSTER, R. Taxonomische Untersuchungen über die Serie *Palustres* M. Pop. der Gattung *Myosotis* L. *Feddes Repert.* **74**: 39–98. 6 pls. 1967. [Thirteen species; cytology, morphology, variation, ecology, distribution, key, maps, new taxa.]
- SOÓ, R., & A. BORHIDI. Über einige Formenkreise der ungarischen und karpatischen Flora. 12. *Myosotis palustris* und *Lamium Galeobdolon*. *Acta Bot. Acad. Sci. Hungar.* **14**: 157–163. 1968.*
- SOUÈGES, R. Embryogénie des Boragacées. Les premiers termes du développement de l'embryon chez le *Myosotis hispida* Schlecht. *Compt. Rend. Acad. Sci. Paris* **173**: 726–728. 1921a.
- . Embryogénie des Boragacées. Les derniers stades du développement de l'embryon chez le *Myosotis hispida* Schlecht. *Ibid.* 848–850. 1921b.
- . Développement de l'embryon chez le *Myosotis hispida* Schlecht. *Bull. Soc. Bot. France* **70**: 385–401. 1923.
- STROH, G. *Myosotis micrantha* Pallas. Ein Beitrag zur Nomenklaturfrage. *Notizbl. Bot. Gart. Berlin* **12**: 471–473. 1935.
- . Die Gattung *Myosotis* L. Versuch einer systematischen Übersicht über die Arten. *Beih. Bot. Centralbl.* **61B**: 317–345. 1941. [Three sections and 104 species; synonymy, distribution, infraspecific taxa, index.]

- SYCHOWA, M. Geographic distribution of the genus *Myosotis* L. in Poland. (In Polish; Latin summary.) *Fragm. Fl. Geobot.* **17**: 477–503. 1971. [Nine species; maps.]
- . The variability of *Myosotis palustris* (L.) Nathh. s. l. in Poland. (In Polish; English summary.) *Ibid.* **21**: 437–457. 1975. [Three species; distribution, maps, key.]
- VAROPOULOS, A. Breeding systems in *Myosotis scorpioides* L. (Boraginaceae). I. Self-incompatibility. *Heredity* **42**: 149–158. 1979. [Self-incompatibility is controlled by polygenic system.]
- VERBERNE, G. Some remarks on the small-flowered forgetmenots. *Acta Bot. Neerl.* **8**: 330–337. 1959. [Nomenclatural notes and distinguishing characters of several closely related species.]
- VESTERGREN, T. Über den Verwandtschaftskreis der *Myosotis versicolor* (Pers.) J. E. Sm. *Sv. Bot. Tidskr.* **24**: 449–467. 1930. [Distribution of three subspecies of *M. versicolor*; notes on *M. Balbisiana* and *M. lutea*.]
- . Systematische Beobachtungen über *Myosotis silvatica* (Ehrh.) Hoffm. und verwandte Formen. *Arkiv Bot.* **29A**(8): 1–39. 1938. [Infraspecific taxonomy of *M. silvatica* and *M. alpestris*; treatment of six other species; new taxa.]
- WADE, A. E. *Myosotis palustris* and its varieties. *Bot. Soc. Exch. Club Brit. Isles* **9**: 157–164. 1930. [Fourteen varieties and eight forms recognized; synonymy, descriptions.]
- . Notes on the genus *Myosotis*. *Jour. Bot. London* **80**: 127–129. 1942. [Typification of *M. scorpioides*, nomenclatural notes on *M. lutea* and *M. repens*.]
- . Plant notes. *Myosotis discolor* Pers. *Watsonia* **2**: 285, 286. 1952. [*M. versicolor* reduced to synonymy of *M. discolor*; new combinations.]
- WELCH, D. Notes on *Myosotis scorpioides* agg. *Watsonia* **6**: 276–279. 1967. [Limits and distinguishing characters of the British aquatic species of *Myosotis*.]
- WILCOX, W. H. A survey of the vascular flora of Crittenden County, Arkansas. *Castanea* **38**: 286–297. 1973. [*M. macrosperma*, *M. micrantha*, *M. verna*, 295.]
- WINSOR, J. A. Variation among midwestern populations of *Myosotis scorpioides* L. (Abstr.) *Am. Jour. Bot.* **72**: 976, 977. 1985. [Midwestern populations believed to represent several European varieties.]

THE GENERA OF PANICEAE (GRAMINEAE: PANICOIDEAE) IN THE SOUTHEASTERN UNITED STATES^{1,2}

WILLIAM J. CRINS³

Tribe PANICEAE R. Br. in Flinders, Voy. Terra Austral. 2: 582. 1814.

Perennials or annuals. Culms unbranched or branched above. Leaves variable in anatomy, exhibiting all known types of kranz anatomy (correlated with various C₄ photosynthetic pathways) or non-kranz anatomy (C₃ photosynthetic pathway), sometimes with transverse veins

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8716834 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8717333 (Carroll E. Wood, Jr., principal investigator). This account, the 137th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. The references I have not seen are marked with an asterisk.

Norton Miller, Carroll Wood, Ihsan Al-Shehbaz, Gordon Tucker, and Barbara Nimblett have provided useful discussion, advice, encouragement, and/or technical assistance. Both Miller and Wood improved the final manuscript with their editing expertise. Thanks are also extended to the staffs of the New York State Library (especially Alta Beach) and the Botanical Libraries of Harvard University (especially Judy Warnement and Holly Bedell) for providing access to many references. I thank the curators of the following herbaria who have sent specimens or provided hospitality and access to the collections under their care during my visits: A, CAN, DAO, GH, MT, and NYS. Several specimens in my personal herbarium were also used in preparing descriptions.

The illustrations used here were published earlier as Figures 10 and 11 in Christopher Campbell's account of the subfamilies and tribes of grasses prepared for the Generic

→

²For an account of the family and its subfamilies and tribes, see C. S. Campbell, The subfamilies and tribes of Gramineae (Poaceae) in the southeastern United States. Jour. Arnold Arb. 66: 123–199. 1985.

³Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230. Present address: Ontario Ministry of Natural Resources, P. O. Box 9000, Huntsville, Ontario P0A 1K0, Canada.

© President and Fellows of Harvard College, 1991.

Journal of the Arnold Arboretum, Supplementary Series 1: 171–312. 1991.

connecting longitudinal veins; with cordate to cuneate or pseudopetiolate blade bases; blades linear to ovate. Inflorescences paniculate, usually terminal, sometimes with additional axillary panicles, open or contracted, primary branches often spike-like, sometimes racemose or digitate, or reduced further to short axes supporting fascicles of spikelets; spikelets all alike [staminate and carpellate or perfect flowers separate in a few genera], 2 flowered, single or in groups of 2 or 3, with or without rachilla extensions, usually dorsiventrally compressed, sometimes terete (e.g., *Lasiacis*) or laterally compressed, disarticulating below the glumes (upper florets rarely disarticulating independently); proximal florets staminate or sterile, with or without palea; distal florets perfect, paleate. Glumes 1 or 2, chartaceous to coriaceous; proximal glumes sometimes vestigial or absent; distal glumes often as long as spikelet. Proximal lemmas chartaceous to coriaceous, not indurate; distal lemmas (and paleas) usually indurate and tightly enclosing caryopses, with germination flap usually conspicuous. Lodicules glabrous (absent in many taxa in subtribe Cenchrinae). Stamens 3 (2). Fruit a caryopsis (grain). Chromosome base numbers 6–11, 17 (9 and 10 most frequent). TYPE GENUS: *Panicum* L.

A large, widely distributed tribe represented in the southeastern United States by 22 genera. The Paniceae R. Br. is one of from two to eleven tribes included by various authors in the subfamily Panicoideae A. Br. Robert Brown's original circumscription of the tribe included genera that are now considered to belong to the tribe Andropogoneae Dumort. However, Bentham, Hackel, and others removed most of the disparate elements, and the tribe's circumscription has remained relatively stable since the late 19th century. Only a few peripheral genera pose problems (e.g., genera included in tribe Isachneae Bentham; Clayton & Renvoize).

The Panicoideae are characterized by dorsiventrally compressed spikelets of two florets each, a staminate or sterile proximal floret, and a perfect distal floret (Campbell). The two largest tribes of the subfamily are the Paniceae and Andropogoneae. Bentham recognized six tribes within his "series Panicaceae" (roughly equivalent to subfamily Panicoideae). Among these was tribe Zoysieae Bentham, which included *Antheophora* Schreber and *Neurachne* R. Br. (both now included in tribe Paniceae) and other genera that belong to subfamily Chloridoideae Rouy. Hackel produced a classification very similar to that of Bentham. Pilger (1940) recognized six subtribes within tribe Paniceae and later elevated several of these to tribal status (Pilger,

Flora (see Footnote 2). Both figures were drawn by Karen Stoutsenberger during a previous grant period (NSF BMS-21469, Carroll E. Wood, Jr., principal investigator) under the supervision of Wood, Kenneth R. Robertson, and Christopher Campbell, who also prepared the materials.

This treatment is published as contribution number 658 of the New York State Science Service.

1954). Clayton & Renvoize used certain components from both of Pilger's systems. They recognized the subtribes Panicinae Stapf (= Setariinae (Dumort.) Dumort.) and Melinidinae (Hitchc.) Pilger from his earlier treatment and tribe Isachneae from his later treatment. However, they also merged a number of Pilger's tribes and subtribes. Butzin (1970) produced a classification for the tribe that has little resemblance to that of Clayton & Renvoize, so it is worthy of a brief discussion. He placed an inordinate amount of significance on the presence or absence of cross-veins in leaves and established subtribe Microcalaminae Butzin to accommodate all genera with this feature. Unfortunately, this meant that many genera with clear affinities to *Panicum* L. were separated from it in his scheme (e.g., *Lasiacis* (Griseb.) Hitchc., *Acroceras* Stapf, *Oplismenus* Beauv., *Sacciolepis* Nash, *Hymenachne* Beauv.). Butzin also recognized or described other subtribes to accommodate small genera that have distinctive autapomorphies but that are otherwise clearly related to larger genera (e.g., subtribes Xerochloinae Butzin, Uranthoeiinae Butzin, Thuareinae Ohwi, Otachyriinae Butzin). Butzin's classification also placed genera that are often considered to be subgenera by other authors into different subtribes. For example, *Phanopyrum* (Raf.) Nash is placed in subtribe Otachyriinae, while *Panicum* is assigned to subtribe Panicinae; *Leptoloma* Chase is placed in subtribe Panicinae, while *Digitaria* Haller is put in subtribe Paspalinae Griseb. emend. Butzin (for which he later provided the name Digitariinae Butzin; Butzin, 1972). Tsvelev (1976) closely followed Butzin's (1970) scheme. However, there seems to be little evolutionary basis for Butzin's classification scheme, and it is best ignored, except when some of the names he validated have priority.

The origins and stimuli for developing a grass classification that reflects evolutionary relationships rather than concentrating on superficial similarities of spikelet structure come from the studies of Prat (1936) and Avdulov. They examined a wide array of character systems and generated classification schemes that were based on syntheses of information from all sources. Avdulov used cytology extensively and added data from endosperm starch-grain micromorphology, leaf anatomy, seedling leaf morphology, and geographical distribution patterns. Prat (1936) examined silica cells, bicellular microhairs, multicellular hairs, the leaf epidermis, embryos, caryopses, and chemistry, and on the basis of all of this evidence he recognized three subfamilies: Festucoideae Rouy (Pooideae A. Br.), Panicoideae, and Bambusoideae Ascherson & Graebner.

Following these extensive surveys, W. V. Brown and his associates (1946 *et seq.*) examined additional character systems, which in general support the subfamilial classification proposed by Prat (1936). Panicoids generally have poorly developed sheath pulvini and well-developed culm pulvini (Brown, Pratt, & Mobley). The organization of the shoot apex of panicoids and pooids tends to differ, with the former usually having a single tunica layer and the latter often with

two tunica layers (Brown, Heimsch, & Emery). Embryological characters of the gametophytes and caryopses provide a large number of differences between the Panicoideae and other subfamilies (Anton de Triquell; Bhanwra; Reeder, 1957; Wang *et al.*). Panicoids generally are capable of germinating at lower oxygen tensions than pooids, chloridoids, and arundinoids (Al-Aish & Brown). Persistent nucleoli in mitotic cells are a common feature in subfamily Panicoideae but not in Pooideae (other subfamilies are variable for this character; Brown & Emery, 1957b). Watson & Johnston have shown that the guard cells of stomata are usually overlapped by adjacent interstomatal cells in subfamily Pooideae, but not in Panicoideae and most other subfamilies.

Some character systems are more useful at the generic and subgeneric levels, e.g., leaf anatomy. In particular, the decarboxylation pathways utilized during photosynthesis have been found to be closely correlated with the anatomy of the vascular bundles in leaves of panicoid genera. Many of the genera have been characterized in terms of these character systems, and disparate elements have been realigned as a result (see Brown 1958a, 1977; Carolin *et al.*; Ellis; Hatch *et al.*; Hattersley, 1984, 1987; Metcalfe; Prendergast & Hattersley).

Parasitism by rust fungi may also prove to be useful in determining relationships within and among subfamilies of the Gramineae. The available evidence suggests that the tribe Paniceae is more advanced than the Andropogoneae (Savile).

Tribe Paniceae is treated here in an inclusive sense. Several segregates that have been accorded tribal rank by others are included as subtribes, following the classifications of Campbell and Clayton & Renvoize.

Tribe Paniceae contains about 90 genera worldwide. The greatest diversity of genera and species is concentrated in the tropics. Relatively few genera include species that extend beyond warm-temperate regions.

Subtribe Neurachninae (S. T. Blake) Clayton & Renvoize (glumes leathery, stigmas 3, distal lemmas membranaceous to leathery) has no representatives in the southeastern United States. Three Australian genera with a total of 10 species constitute this group. Leaf anatomy is variable, even within a genus (*Neurachne* R. Br. contains non-kranz and kranz species). Clayton & Renvoize suggest that this subtribe is an early derivative from the ancestral lineage.

Subtribe Digitariinae Butzin (inflorescence usually composed of digitate, racemose branches with secund spikelets, proximal glume usually small or absent, distal lemma with flat, thin margins enclosing most or all of distal palea) contains two genera with representatives in the Southeast, *Digitaria* and *Anthaenantia* Beauv. A majority of the genera in the subtribe has kranz leaf anatomy of the mestome sheath type. Clayton & Renvoize proposed that this subtribe diverged early from subtribe Setariinae. In their diagram of relationships, subtribe Digitariinae falls between subtribes Neurachninae and Setariinae.

Subtribe Arthropogoninae Butzin is a small group containing two genera, *Arthropogon* Nees and *Reynaudia* Kunth, of the West Indies and Brazil. Neither genus has representatives in the Southeast.

The subtribe is unusual in the Paniceae in having laterally compressed spikelets (but there are a few examples in other subtribes) and hyaline distal floret bracts. The leaf anatomy of *Arthropogon* appears to be intermediate between non-kranz and kranz types (Clayton & Renvoize). Clayton & Renvoize concluded that the subtribe is an offshoot of the Digitariinae and is probably most closely related to *Anthaeantia* (particularly those species placed by some authors in *Leptocoryphium* Nees).

Members of subtribe Cenchrinae (Dumort.) Dumort.⁴ (including Anthephorinae Benth) have bristles or scales (often fused to varying degrees) that subtend spikelets or fascicles of spikelets and are deciduous with the spikelets. These genera differ from other bristle-bearing ones (e.g., *Setaria* Beauv.) in which the spikelets are deciduous but the bristles persist on the inflorescence axes. Genera in subtribe Cenchrinae also have soft distal lemmas, suggesting a relationship with subtribe Digitariinae, but not with Setariinae (Clayton & Renvoize).

Subtribe Setariinae (Panicinae Stapf, Paspalinae Griseb., Brachiariinae Butzin) is the largest subtribe of Paniceae in the Southeast and in the world. Some of the largest genera of angiosperms (including *Panicum* and *Paspalum* L.) are in this subtribe. The other genera with members in our area are *Oplismenus*, *Lasiacis*, *Amphicarpum* Kunth, *Hymenachne*, *Sacciolepis*, *Echinochloa* Beauv., *Alloteropsis* Presl, *Urochloa* Beauv., *Eriochloa* Kunth, *Reimarochloa* Hitchc., *Axonopus* Beauv., *Setaria*, *Paspalidium* Stapf, and *Stenotaphrum* Trin. The unifying character for the subtribe is the indurate distal lemma, which has involute margins covering the edges of the palea. The subtribe is extremely diverse in the structure of its foliage (non-kranz and all known forms of kranz anatomy are represented), but the spikelets are structurally uniform. Even within *Panicum*, non-kranz and both parenchyma-sheath and mestome-sheath subtypes of kranz anatomy are found. Several genera that appear to be derivatives of *Panicum* are here retained as genera (e.g., *Lasiacis*, *Amphicarpum*, *Sacciolepis*). However, phylogenetic analyses may indicate that these segregates render *Panicum* paraphyletic, and generic and infrageneric classifications may require realignments in the face of such evidence. This is a topic that requires much more attention.

Subtribe Melinidinae (often treated as tribe Melinideae Hitchc.) (inflorescences paniculate, spikelets laterally compressed, proximal glumes reduced, distal floret bracts hardened) contains two genera, *Melinis* Beauv. (including *Rhynchelytrum* Nees and *Mildbraediochloa* Butzin) and *Tricholaena* Schrader ex Schultes (Zizka). Clayton & Renvoize consider the subtribe to have been derived from a lineage within

⁴When Dumortier (1824) described the taxon "Cenchreae" as a subunit of tribe Paniceae, he did not designate a formal rank. Later, he (1827) applied the rank of subtribe explicitly. Therefore, the citation for this taxon must be subtribe Cenchrinae (Dumort.) Dumort.

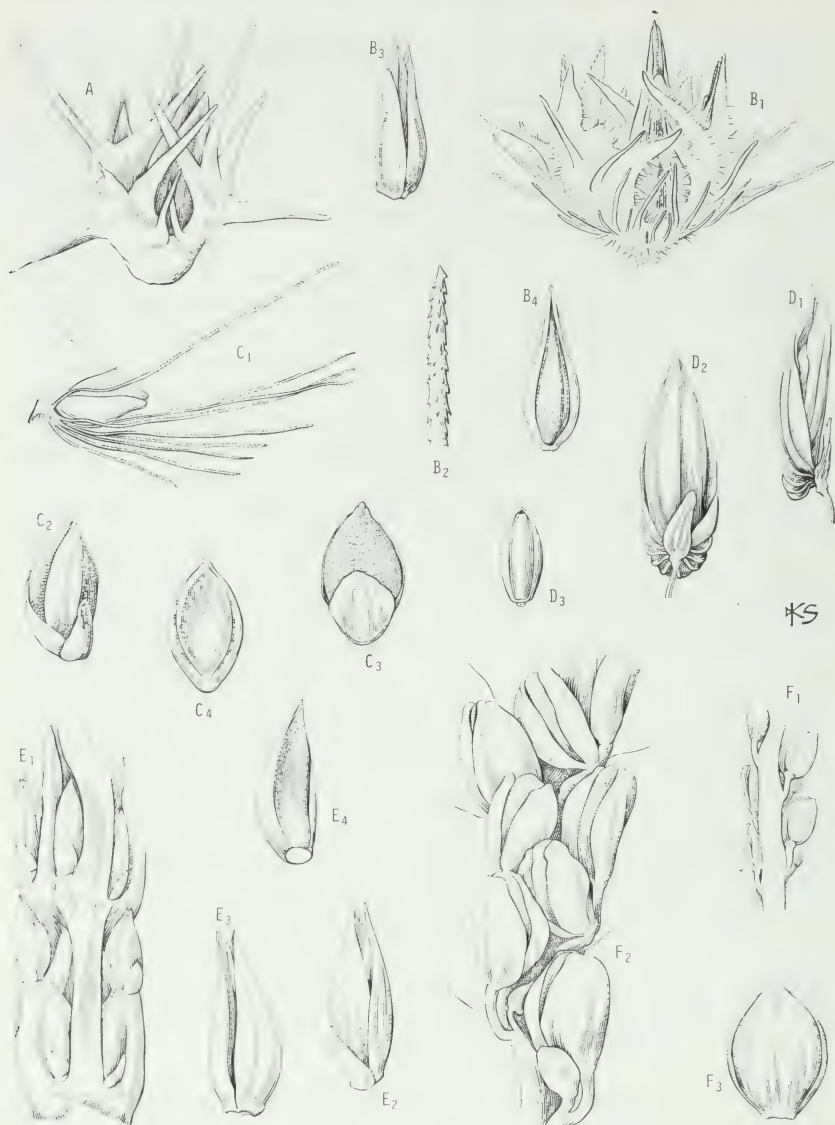


FIGURE 1. Inflorescences, spikelets, and their parts, **Paniceae**. A, B, subtribe **CENCHRINAE**: A, *Cenchrus gracillimus*: involucre with spikelets, $\times 5$. B, *Cenchrus echinata*: B₁, involucre with spikelets, $\times 5$; B₂, tip of spine from involucre, $\times 25$; B₃, spikelet, $\times 5$; B₄, floret, palea to front, lemma behind, $\times 5$. C–F, subtribe **SETARIINAE**: C, *Setaria geniculata*: C₁, spikelet with subtending bristles, $\times 5$; C₂, spikelet, showing 2 glumes, sterile lemma to right, fertile lemma to left (slightly rugose), $\times 10$; C₃, spikelet, showing second glume and slightly rugose indurated lemma of fertile floret, $\times 10$; C₄, fertile floret, lemma clasping palea, $\times 10$. D, *Sacciolepis striata*, $\times 10$; D₁, spikelet, showing 2 glumes and lemma of sterile floret;

Panicum that has parenchyma bundle-sheaths. Under this hypothesis, not only *Panicum* but the entire subtribe Setariinae, would be paraphyletic.

Subtribe Spinificinae Ohwi consists of only three genera (*Xerochloa* R. Br., *Zygochloa* S. T. Blake, *Spinifex* L.) that occur in arid habitats from Australia to China and India. They have compact, compound inflorescences. Some species are dioecious. The genera possess an array of apomorphies related to dispersal, including 'tumbleweed' inflorescences (*Spinifex*), papery 'bracts' that aid in wind dispersal (*Zygochloa*), or hardened, falcate, beaked distal lemma apices that assist in adhesion (*Xerochloa*). Clayton & Renvoize suggest a relationship with *Uranthoecium* Stapf (subtribe Setariinae).

It is evident that serious problems still exist in evolutionary interpretation and resultant classification schemes of the Paniceae and its component parts. A cladistic analysis at the family level (Kellogg & Campbell) indicates that subfamily Panicoideae is monophyletic, but relationships within the subfamily have yet to be analyzed in this way. Although the tribal, subtribal, and generic classification scheme presented by Clayton & Renvoize is practical, it will undoubtedly be improved when phylogenetic considerations based on cladistic analyses are incorporated. Only then will there be a clear idea of whether the numerous segregates of *Panicum* deserve generic status, and whether the subtribes are based on true apomorphies. Little advancement in the understanding of infratribal relationships will occur until such analyses are made.

Polyploidy is a characteristic feature of almost all genera in the Paniceae. Aposporous reproduction, coupled with pseudogamy, is often associated with the polyploid state. In aposporous taxa, the embryo sac may be either 4- or 8-nucleate (Brown & Emery, 1958; Pritchard). Aneuploidy is less common, but is known to occur in several genera of the tribe. These aspects of cytology and reproductive biology are considered in more detail under the individual generic treatments.

Although very few species have been examined, panicoids (Paniceae and Andropogoneae) have consistently low hydrocarbon content (Buchanan *et al.*). All investigated species are similar in their amino acid profiles, with high levels of alanine and leucine, and low levels of lysine, arginine, and glutamic acid (Taira; Yeoh & Watson). Paniceae are intermediate between subfamily Chloridoideae and tribe Andropogoneae in levels of glutamic acid and proline (Yeoh & Watson).

D₂, same, turned 90° to show shape of sterile lemma and glumes; D₃, fertile floret, showing lemma clasping palea. E, *Stenotaphrum secundatum*: E₁, section of flattened, thickened rachis, showing partially embedded spikelets, ×3; E₂, spikelet, first glume to left, ×6; E₃, spikelet with glumes removed, fertile (upper) floret to right, sterile floret to left, ×6; E₄, fertile floret, showing lemma to left, ×12. F, *Paspalum floridanum*: F₁, section of rachis, ×2; F₂, section of rachis from other side, showing spikelets in pairs, 1 spikelet of each of 2 lowest pairs aborted, ×5; F₃, fertile floret, lemma behind, inrolled margins clasping palea, ×5.

Several genera in the tribe contain species of significant economic importance. The sixth most important cereal crop in the world is pearl millet, *Pennisetum americanum* (L.) Leeke (Jauhar). Species of *Panicum*, *Paspalum*, and *Urochloa* are major forage and grain crops. *Stenotaphrum secundatum* (Walter) Kuntze is an important tropical turf grass. In addition, species in many genera of the Paniceae are major components of grassland, wetland, and forest edge communities throughout the warmer parts of the world. Several species of *Echinochloa*, *Panicum*, and *Setaria* are also serious weeds in agricultural systems.

REFERENCES:

- ADANSON, M. Familles des plantes. 2 vols. 640 pp. Paris. 1763-1764.
- AL-AISH, M., & W. V. BROWN. Grass germination responses to isopropyl-phenyl carbamate and classification. Am. Jour. Bot. **45**: 16-23. 1958. [Panicoids germinate at much lower oxygen tensions than pooids.]
- ANDERSON, L. C. Noteworthy plants from North Florida. III. Sida **13**: 93-100. 1988. [*Eriochloa Michauxii* (Poirot) Hitchc. and *Setaria viridis* (L.) Beauv. from Franklin Co.]
- ANTON DE TRIQUELL, A. Grass gametophytes: their origin, structure, and relation with the sporophyte. Pp. 11-20 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D.C. 1987.
- ARBER, A. Studies in the Gramineae. X. 1. *Pennisetum*, *Setaria*, and *Cenchrus*. 2. *Alopecurus*. 3. *Lepturus*. Ann. Bot. **45**: 401-421. 1931.
- . The Gramineae: A study of cereal, bamboo, and grass. xvii + 480 pp. Cambridge, England. 1934.
- ARROYO, J. A., & L. R. BRENES. Digestibility studies on Napier (Merker) grass (*Pennisetum purpureum*), giant pangolagrass (*Digitaria valida* Stent), and signalgrass (*Brachiaria brizantha*). Jour. Agr. Univ. Puerto Rico **45**: 151-156. 1961. [*P. purpureum* and *B.* (= *Urochloa*) *brizantha* much higher in dry matter content at 50 days of age than *D. valida*.]
- AVDULOV, N. P. Karyo-systematische Untersuchung der Familie Gramineen. (In Russian; German summary.) Trudy Prikl. Bot. Genet. Selektiv. Prilozh. **44**: 3-428. 1931.
- BAQUAR, S. R., & M. SAEED. Chromosome studies and polyploidy analysis in grasses of West Pakistan. I. Caryologia **22**: 103-111. 1969. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Echinochloa*, *Panicum*, *Paspalidium*, *Paspalum*, *Setaria*.]
- BENTHAM, G. Notes on Gramineae. Jour. Linn. Soc. Bot. **19**: 14-134. 1882. [An enlightened and critical commentary on grass systematics for its time; contains a classification of tribes with full descriptions and ample discussion.]
- BEWS, J. W. The world's grasses. xii + 408 pp. London. 1929. [Melinideae, 123, 124; Paniceae, 124-130; discussion of distribution, ecology, economic importance of many genera.]
- BHANWRA, R. K. Embryology in relation to systematics of Gramineae. Ann. Bot. II. **62**: 215-233. 1988. [Pooid and panicoid embryos compared on basis of several morphological and anatomical characters.]
- BIR, S. S., & M. SAHNI. Cytological investigations on some grasses from Punjab Plain, North India. Proc. Indian Natl. Sci. Acad. **51B**: 609-626. 1985. [Chromosome counts and observations of meiotic irregularities in *Cenchrus*, *Digitaria*, *Echinochloa*, *Panicum*, *Setaria*, *Urochloa*.]

- BLAKE, S. T. New criteria for distinguishing genera allied to *Panicum* (Gramineae). Proc. Roy. Soc. Queensland **70**: 15-19. 1958. [Surface sculpturing, orientation and shape of distal forelet, and germination flap of distal lemma useful in distinguishing among *Brachiaria*, *Entolasia*, *Eriochloa*, *Ottlochloa*, *Panicum*, *Paractaenum*, *Paspalidium*, *Setaria*, *Urochloa*.]
- BLOMQUIST, H. L. The grasses of North Carolina. vi + 276 pp. Durham, North Carolina. 1948. [Paniceae, 119-193.]
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. In: A. A. FEDEROV, ed., Chromosome numbers of flowering plants. (Russian and English prefaces.) 926 pp. Leningrad. 1969.
- BOR, N. L. The grasses of Burma, Ceylon, India and Pakistan (excluding Bambuseae). xviii + 767 pp. New York. 1960. [Paniceae, 271-373.]
- BOWDEN, W. M., & H. A. SENN. Chromosome numbers in 28 grass genera from South America. Canad. Jour. Bot. **40**: 1115-1124. 1962. [Counts in *Cenchrus*, *Paspalum*, *Setaria*.]
- BRENES, L. R., J. A. ARROYO, H. CESTERO, & A. SIERRA. Palatability tests on giant pangola grass (*Digitaria valida* Stent) and signal grass (*Brachiaria brizantha*) as compared with Napier (Merker) grass (*Pennisetum purpureum*). Jour. Agr. Univ. Puerto Rico **45**: 147-150. 1961. [*D. valida* and *B.* (= *Urochloa*) *brizantha* are as palatable as *P. purpureum*, one of the most palatable grasses in Puerto Rico.]
- BROWN, R. General remarks, geographical and systematical, on the botany of Terra Australis. Pp. 533-613 in FLINDERS, M., A voyage to Terra Australis. Vol. II. 1814. [Original description of tribe Paniceae; discussion of its diversity in the tropics.]
- BROWN, W. V. A cytological study in the Paniceae. (Abstr.) Am. Jour. Bot. **33**: 818. 1946. [Chromosome counts in *Amphicarpum*, *Axonopus*, *Cenchrus*, *Digitaria*, *Echinochloa*, *Leptoloma* (= *Digitaria*), *Oplismenus*, *Panicum*, *Paspalum*, *Sacciolepis*, *Setaria*, *Stenotaphrum*.]
- . A cytological study in the Gramineae. *Ibid.* **35**: 382-395. 1948. [Chromosome counts in *Amphicarpum*, *Axonopus*, *Cenchrus*, *Digitaria*, *Echinochloa*, *Leptoloma* (= *Digitaria*), *Oplismenus*, *Panicum*, *Paspalum*, *Sacciolepis*, *Setaria*, *Stenotaphrum*.]
- . A cytological study of some Texas Gramineae. Bull. Torrey Bot. Club **77**: 63-76. 1950. [Chromosome counts in *Axonopus*, *Cenchrus*, *Echinochloa*, *Eriochloa*, *Panicum*, *Paspalum*, *Setaria*, *Stenotaphrum*.]
- . Chromosome numbers of some Texas grasses. *Ibid.* **78**: 292-299. 1951. [Counts in *Eriochloa*, *Leptoloma* (= *Digitaria*), *Panicum*, *Paspalum*, *Stenotaphrum*, *Trichachne* (= *Digitaria*).]
- . Leaf anatomy in grass systematics. Bot. Gaz. **119**: 170-178. 1958a. [Six basic types characterized: festucoid, bambusoid, arundinoid, panicoid, aristoid, chloroid.]
- . Apomixis as related to geographical distribution in the panicoid grass tribes. Jour. S. Afr. Bot. **24**: 191-200. 1958b. [*Cenchrus*, *Echinochloa*, *Eriochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*; high frequency of apomicts in the Panicoideae.]
- . The epiblast and coleoptile of the grass embryo. Bull. Torrey Bot. Club **86**: 13-16. 1959.
- . The kranz syndrome and its subtypes in grass systematics. Mem. Torrey Bot. Club **23**(3): 1-97. 1977. [Excellent synthesis of the systematic importance of leaf anatomy and physiology.]
- & W. H. P. EMERY. Some South African apomictic grasses. Jour. S. Afr. Bot. **23**: 123-125. 1957a. [*Antheophora*, *Panicum*, *Pennisetum*, *Urochloa*.]
- & ———. Persistent nucleoli and grass systematics. Am. Jour. Bot. **44**: 585-590. 1957b. [All panicoids have persistent nucleoli in some, but not all, cells; no persistent nucleoli in pooids.]

- & ———. Apomixis in the Gramineae: Panicoideae. *Ibid.* **45**: 253–263. 1958. [*Antheophora*, *Brachiaria*, *Eriochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Urochloa* contain species with 4-nucleate embryo sacs; *Axonopus*, *Brachiaria*, *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Leptoloma* (= *Digitaria*), *Panicum*, *Paspalum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Stenotaphrum* contain species with normal (8-nucleate) embryo sacs.]
- , W. F. HARRIS, & J. D. GRAHAM. Grass morphology and systematics. I. The internode. *Southwest. Nat.* **4**: 115–125. 1959. [*Antheophora*, *Cenchrus*, *Digitaria*, *Eriochloa*, *Leptoloma* (= *Digitaria*), *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*, *Stenotaphrum*, *Trichachne* (= *Digitaria*), *Urochloa*.]
- , C. HEIMSCH, & W. H. P. EMERY. The organization of the grass shoot apex and systematics. *Am. Jour. Bot.* **44**: 590–595. 1957. [Two tunica layers in most pooids, one layer in most panicoids, but some genera (e.g., *Panicum*) variable.]
- , G. A. PRATT, & H. M. MOBLEY. Grass morphology and systematics. II. The nodal pulvinus. *Southwest. Nat.* **4**: 126–130. 1959. [Culm pulvinus generally present in panicoids, absent in pooids; sheath pulvinus less developed in panicoids than pooids.]
- & B. N. SMITH. Grass evolution, the kranz syndrome, $^{13}\text{C}/^{12}\text{C}$ ratios, and continental drift. *Nature* **239**: 345–346. 1972. [Kranz-type Paniceae dominant in South America; all non-kranz species should be removed from *Panicum*.]
- BUCHANAN, R. A., C. L. SWANSON, D. WEISLEDER, & I. M. CULL. Gutta-producing grasses. *Phytochemistry* **18**: 1069–1071. 1979. [Panicoids consistently low in hydrocarbons.]
- BURTON, G. W. A cytological study of some species in the tribe Paniceae. *Am. Jour. Bot.* **29**: 355–359. 1942. [Chromosome counts in *Axonopus*, *Digitaria*, *Panicum*, *Paspalum*, *Pennisetum*; most material from Florida.]
- BUTZIN, F. Die systematische Gliederung der Paniceae. *Willdenowia* **6**: 179–192. 1970. [Artificial subtribal classification scheme.]
- . Digitariinae, ein neuer Subtribusname bei den Paniceae. *Ibid.* **6**: 509, 510. 1972.
- . Die Namen der supragenerischen Einheiten der Gramineae (Poaceae). *Ibid.* **7**: 113–168. 1973. [A listing of names, many not published at the rank indicated, others nomina nuda.]
- CAMPBELL, C. S. The subfamilies and tribes of Gramineae (Poaceae) in the south-eastern United States. *Jour. Arnold Arb.* **66**: 123–199. 1985.
- , J. A. QUINN, G. P. CHEPLICK, & T. J. BELL. Cleistogamy in grasses. *Ann. Rev. Ecol. Syst.* **14**: 411–441. 1983. [*Amphicarpum*, *Panicum*, *Paspalum*.]
- CARNAHAN, H. L., & H. D. HILL. Cytology and genetics of forage grasses. *Bot. Rev.* **27**: 1–162. 1961. [Interspecific hybrids in *Digitaria*, *Paspalum*, *Pennisetum*; no original chromosome counts.]
- CAROLIN, R. C., S. W. L. JACOBS, & M. VESK. The structure of the cells of the mesophyll and parenchymatous bundle sheath of the Gramineae. *Bot. Jour. Linn. Soc.* **66**: 259–275. 1973. [Detailed description of panicoid leaf anatomy.]
- CHANDOLA, R. P. Cyto-genetics of millets (1). *Cytologia* **24**: 115–137. 1959. [Chromosome counts, pollen sterility, meiotic figures in species of *Panicum* (= *Echinochloa* spp., *Urochloa* sp.), *Pennisetum*, *Setaria*.]
- CHASE, A. Notes on genera of Paniceae. I. *Proc. Biol. Soc. Wash.* **19**: 183–192. 1906. [Fruits of type species of *Anthraenantia* Beauv., *Leptocoryphium* Nees, *Leptoloma* Chase, *Syntherisma* Walter, *Valota* Adanson illustrated; *Leptoloma* described.]
- . Notes on genera of Paniceae. II. *Ibid.* **21**: 1–10. 1908. [Differences between *Hymenachne* and *Sacciolepis*.]
- . Notes on genera of Paniceae. IV. *Ibid.* **24**: 103–159. 1911. [Lectotypification of many genera.]

- CHEN, C.-C., & C.-C. HSU. Cytological studies on Taiwan grasses. I. Tribe Paniceae. Bot. Bull. Acad. Sinica II. 2: 101-110. 1961. [Chromosome counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Oplismenus*, *Panicum*, *Paspalum*, *Pennisetum*, *Sacciolepis*, *Setaria*.]
- CHIPPINDALL, L. K. A. A guide to the identification of grasses in South Africa. Pp. 1-527 in D. MEREDITH, ed., The grasses and pastures of South Africa. Parow, South Africa. 1955. [Much useful information, insightful discussions of taxonomic problems, good keys and illustrations.]
- CHURCH, G. L. Meiotic phenomena in certain Gramineae. II. Paniceae and Andropogoneae. Bot. Gaz. 88: 63-84. 1929. [Chromosome numbers and observations of meiotic phenomena in *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*.]
- . Cytotaxonomic studies in the Gramineae. *Spartina*, *Andropogon* and *Panicum*. Am. Jour. Bot. 27: 263-271. 1940. [*Panicum virgatum*, $2n = 36$ or 72.]
- CLARK, C. A., & F. W. GOULD. Some epidermal characteristics of paleas of *Dichanthelium*, *Panicum*, and *Echinochloa*. Am. Jour. Bot. 62: 743-748. 1975.
- CLAYTON, W. D. Some new African grasses. Kew Bull. 30: 557-560. 1980. [Various taxa previously assigned to *Brachiaria* are reassigned to *Acroceras* and *Echinochloa*; new names and combinations provided for species of *Brachiaria* (= *Urochloa*), *Echinochloa*, *Eriochloa*.]
- & S. A. RENVOIZE. Genera graminum. Grasses of the world. Kew Bull. Additional Ser. 13. 389 pp. 1986. [Excellent compendium, with workable keys; inadequate justifications for some generic circumscriptions.]
- CLEWELL, A. F. Guide to the vascular plants of the Florida Panhandle. 605 pp. Tallahassee, Florida. 1985.
- CONNOR, H. E. Evolution of reproductive systems in the Gramineae. Ann. Missouri Bot. Gard. 68: 48-74. 1981. [Breeding systems; all grasses.]
- . Reproductive biology in grasses. Pp. 117-132 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D. C. 1987.
- DAHLGREN, R. M. T., H. T. CLIFFORD, & P. F. YEO. The families of the monocotyledons. Structure, evolution, and taxonomy. xi + 520 pp. Berlin. 1985.
- DARLINGTON, C. D., & E. K. JANAKI AMMAL. Chromosome atlas of cultivated plants. 397 pp. London. 1945. [Paniceae, 329-332.]
- & A. P. WYLIE. Chromosome atlas of flowering plants. xix + 519 pp. London. 1955. [Paniceae, 423-428.]
- DAVIDSE, G. Fruit dispersal in the Poaceae. Pp. 143-155 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D.C. 1987. [One of the few sources of information on the dispersal of grass propagules; largely speculative, but still useful.]
- , T. HOSHINO, & B. K. SIMON. Chromosome counts of Zimbabwean grasses (Poaceae) and an analysis of polyploidy in the grass flora of Zimbabwe. S. Afr. Jour. Bot. 52: 521-528. 1986. [Counts in *Digitaria*, *Oplismenus*, *Panicum*, *Rhynchelytrum* (= *Melinis*), *Sacciolepis*, *Setaria*, *Urochloa*; 45 percent of Zimbabwean grasses show infraspecific polyploidy.]
- & R. W. POHL. Chromosome numbers and notes on some Central American grasses. Canad. Jour. Bot. 50: 273-283. 1972a. [Counts in *Axonopus*, *Panicum*, *Paspalum*, *Pennisetum*; cleistogamous flowers in secondary panicles (like those of *Panicum* subg. *Dichanthelium*) in *Panicum panatrichum* Hackel.]
- & ———. Chromosome numbers, meiotic behavior, and notes on some grasses from Central America and the West Indies. *Ibid.* 1441-1452. 1972b. [Chromosome counts in *Axonopus*, *Brachiaria* (= *Urochloa*), *Echinochloa*, *Eriochloa*, *Panicum*, *Paspalum*, *Setaria*, *Trichachne* (= *Digitaria*); meiotic irregularities in *Brachiaria* (laggards), *Eriochloa* (univalents, laggards), *Paspalum* (univalents, trivalents).]

- & ———. Chromosome numbers, meiotic behavior, and notes on tropical American grasses (Gramineae). *Ibid.* 52: 317–328. 1974. [Counts in *Ar-enopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Hymenachne*, *Oplismenus*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*.]
- DAWSON, J. H., & V. F. BRUNS. Longevity of barnyardgrass, green foxtail, and yellow foxtail seeds in soil. *Weed Sci.* 23: 437–440. 1975. [Considerable variability in all species.]
- DENGLER, N. G., R. E. DENGLER, & P. W. HATTERSLEY. Differing ontogenetic origins of PCR ("kranz") sheaths in leaf blades of C₄ grasses (Poaceae). *Am. Jour. Bot.* 72: 284–302. 1985. [In grasses with double sheaths, the PCR sheath is homologous with the parenchyma bundle sheath of C₃ grasses; in single-sheath C₄ grasses, the sheath is homologous with the mesotome sheath.]
- DE WET, J. M. J. Chromosome numbers of a few South African grasses. *Cytologia* 19: 97–103. 1954. [Counts in *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Urochloa*.]
- . Additional chromosome numbers in Transvaal grasses. *Ibid.* 23: 113–118. 1958. [Counts in *Alloteropsis*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Oplismenus*, *Panicum*, *Paspalum*, *Setaria*.]
- . Chromosome numbers and some morphological attributes of various South African grasses. *Am. Jour. Bot.* 47: 44–49. 1960. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Eriochloa*, *Panicum*, *Paspalidium*, *Pennisetum*, *Sacciolepis*.]
- & L. J. ANDERSON. Chromosome numbers in Transvaal grasses. *Cytologia* 21: 1–10. 1956. [Chromosome counts in *Alloteropsis*, *Antheophora*, *Ar-onopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Urochloa*.]
- DUDECK, A. E., & C. H. PEACOCK. Companion grass and mulch influences on Bahiagrass, centipedegrass, and St. Augustin grass establishment. *Jour. Am. Soc. Hort. Sci.* 111: 844–848. 1986. [*Paspalum notatum* var. *saurae* Parodi, *Eremochloa ophiuroides* (Munro) Hackel, *Stenotaphrum secundatum* (Walter) Kuntze.]
- DUJARDIN, M. In: IOPB chromosome number reports. LXIII. *Taxon* 28: 265–279. 1979. [Counts in *Ar-onopus*, *Brachiaria* (= *Urochloa*), *Digitaria*, *Panicum* (incl. species of *Urochloa*), *Rhynchelytrum* (= *Melinis*), *Setaria*.]
- DUMORTIER, B. C. J. Observations sur les Graminées de la flore belgeque. viii + 153 pp. Tournay. 1824.
- . *Florula Belgica*. iii + 172 pp. Tournay. 1827. [Subtribes explicitly designated for the first time in grasses.]
- DUNCAN, W. H. Three grasses new to Georgia: *Eriochloa gracilis*, *Setaria Faberii*, *Leptochloa uninervia* (Gramineae). *Sida* 5: 42, 43. 1972.
- EASTMAN, P. A. K., N. G. DENGLER, & C. A. PETERSON. Suberized bundle sheaths in grasses (Poaceae) of different photosynthetic types. I. Anatomy, ultrastructure and histochemistry. *Protoplasma* 142: 92–111. 1988a. [In grasses utilizing the NADP-malic enzyme type of acid decarboxylation (one of the C₄ pathways), the parenchyma bundle sheath is the only continuous sheath around the vascular bundle; in the NAD-malic enzyme and PEP-carboxy kinase types, both parenchyma bundle sheath and mesotome sheath are continuous; includes *Panicum capillare* (NAD-me), *Setaria glauca* (NADP-me), *Echinochloa crus-galli* (NADP-me), as well as grasses from other tribes.]
- , C. A. PETERSON, & N. G. DENGLER. Suberized bundle sheaths in grasses (Poaceae) of different photosynthetic types. II. Apoplastic permeability. *Ibid.* 112–126. 1988b. [Solutes of small size penetrate both mesotome sheath and parenchyma bundle sheath of all veins of all photosynthetic types.]
- EDGAR, E., & J. E. SHAND. Checklist of panicoid grasses naturalised in New Zealand; with a key to native and naturalised genera and species. *New Zealand Jour. Bot.* 25: 343–353. 1987.

- ELLIS, R. P. A review of comparative leaf blade anatomy in the systematics of the Poaceae: the past twenty-five years. Pp. 1-10 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D.C. 1987.
- FERNALD, M. L. Some transfers in *Digitaria* and *Paspalum*. *Rhodora* **36**: 19-22. 1934. [*D. filiformis* var. *villosa* (Nash) Fern.; *P. ciliatifolium* var. *Muhlenbergii* (Nash) Fern.; *P. ciliatifolium* var. *stramineum* (Nash) Fern.]
- FERNANDES, A., & M. QUEIRÓS. Contribution à la connaissance cytotaxinomique des Spermatophyta du Portugal. I. Gramineae. *Bol. Soc. Brot.* **II. 43**: 20-145. 1969. [Chromosome counts in *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*.]
- GADELLA, T. W. J. In: IOPB chromosome number reports. LVI. *Taxon* **26**: 257-274. 1977. [Counts in *Digitaria*, *Setaria*.]
- GAMALEI, Y. V., & E. V. VOZNESENSKAYA. Structural biochemical types of C-4 plants. *Soviet Pl. Physiol.* **33**: 616-630. 1986. [Paniceae contains three biochemical types.]
- GEBAUER, G., B. SCHUBERT, M. I. SCHUHMACHER, H. REHDER, & H. ZIEGLER. Biomass production and nitrogen content of C₃- and C₄-grasses in pure and mixed culture with different nitrogen supply. *Oecologia* **71**: 613-617. 1987. [C₄ grasses suffer most under nitrogen starvation.]
- GIBBS RUSSELL, G. E. Correlation between evolutionary history, flowering phenology, growth form and seral status for important veld grasses. *S. Afr. Jour. Bot.* **2**: 175-180. 1983. [All species at late successional stages are panicoids and are better adapted to the more mesic conditions of unused (ungrazed) veld; all early-flowering panicoids are in late seral stages.]
- GOEBEL, K. Beiträge zur Entwicklungsgeschichte einiger Inflorescenzen. *Jahrb. Wiss. Bot.* **14**: 1-42. 1884. [Illustrations of spikelet structure of *Setaria*, Figs. 7-18; *Pennisetum*, Figs. 19-21; *Cenchrus*, Figs. 22-29; *Antheophora*, Figs. 46-53.]
- GOULD, F. W. Chromosome numbers in southwestern grasses. *Am. Jour. Bot.* **45**: 757-767. 1958. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum* (= *Cenchrus*) *ciliare*, *Setaria*]; *II. Ibid.* **47**: 873-877. 1960. [Counts in *Cenchrus*, *Digitaria*, *Leptoloma* (= *Digitaria*), *Panicum*, *Paspalum*, *Setaria*, *Urochloa*.]
- . Chromosome numbers of some Mexican grasses. *Canad. Jour. Bot.* **44**: 1683-1696. 1966. [Counts in *Antheophora*, *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Leptoloma* (= *Digitaria*), *Panicum*, *Paspalum*, *Setaria*.]
- . New name combinations for some North American grasses. *Southwest. Nat.* **15**: 391, 392. 1971. [New combinations in *Echinochloa*, *Leptoloma* (= *Digitaria*), *Paspalidium*.]
- . The grasses of Texas. viii + 653 pp. College Station, Texas. 1975. [Paniceae, 406-567.]
- . Poaceae. Pp. 25-220 in R. A. HOWARD, Fl. Lesser Antilles. Vol. 3. Monocotyledoneae. Jamaica Plain, Massachusetts. 1979. [Paniceae, 29, 30, 95-184.]
- & R. B. SHAW. Grass systematics. 2nd ed. ix + 397 pp. College Station, Texas. 1983. [Paniceae, 212-246.]
- & T. R. SODERSTROM. Chromosome numbers of tropical American grasses. *Am. Jour. Bot.* **54**: 676-683. 1967. [Counts in *Axonopus*, *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Lasiacis*, *Panicum*, *Paspalum*, *Rhynchelytrum* (= *Melinis*), *Sacciolepis*, *Setaria*.]
- & ———. In: IOPB chromosome number reports. XXV. *Taxon* **19**: 102-113. 1970a. [Counts in *Cenchrus*, *Digitaria*, *Pennisetum*.]
- & ———. Chromosome numbers of some Mexican and Colombian grasses. *Canad. Jour. Bot.* **48**: 1633-1639. 1970b. [Counts in *Axonopus*, *Cenchrus*, *Digitaria*, *Eriochloa*, *Hymenachne*, *Lasiacis*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*.]

- GUPTA, P. K. Meiotic studies in some members of the tribe Paniceae. *Curr. Sci. Bangalore* **32**: 180, 181. 1963. [Chromosome counts in *Alloteropsis*, *Echinochloa*, *Panicum*, *Paspalidium*, *Paspalum*, *Pennisetum*, *Setaria*.]
- . In: IOPB chromosome number reports. XX. *Taxon* **18**: 213–221. 1969. [Counts in *Alloteropsis*, *Brachiaria* (= *Urochloa*), *Digitaria*, *Panicum*, *Paspalidium*, *Paspalum*, *Pennisetum*, *Setaria*.]
- & YASHVIR. In: IOPB chromosome number reports. XXXII. *Ibid.* **20**: 349–356. 1971. [Counts in *Cenchrus*, *Panicum*, *Setaria*.]
- GUTIERREZ, M., V. E. GRACEN, & G. E. EDWARDS. Biochemical and cytological relationships in C₄ plants. *Planta* **119**: 279–300. 1974. [Three acid decarboxylation types and their anatomical correlates in *Cenchrus*, *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*, *Urochloa*.]
- HACKEL, E. Gramineae (echte Gräser). In A. ENGLER & K. PRANTL, eds., *Nat. Pflanzenfam.* II. **2**: 1–97. 1887. [Hierarchical classification of family, including descriptions and new combinations at subtribal, subgeneric, sectional ranks.]
- HALL, D. W. The grasses of Florida. vi + 496 pp. Ph.D. dissertation, Univ. Florida, Gainesville. 1978.
- HANSON, C. G., & J. L. MASON. Bird seed aliens in Britain. *Watsonia* **15**: 237–252. 1985. [Numerous Paniceae grow spontaneously or have been germinated from mixtures of bird seed.]
- HARBORNE, J. B., & C. A. WILLIAMS. Flavonoid patterns in grasses. Pp. 107–113 in T. R. SODERSTROM *et al.*, eds., *Grass systematics and evolution*. Washington, D.C. 1987.
- HARRIS, T. C., & R. L. RITTER. Giant green foxtail (*Setaria viridis* var. *major*) and fall panicum (*Panicum dichotomiflorum*) competition in soybeans (*Glycine max*). *Weed Sci.* **35**: 663–668. 1987.
- HATCH, M. D., T. KAGAWA, & S. CRAIG. Subdivision of C₄-pathway species based on differing C₄ acid decarboxylating systems and ultrastructural features. *Austral. Jour. Pl. Physiol.* **2**: 111–128. 1975. [*Digitaria sanguinalis* (L.) Scop. and *Pennisetum typhoides* (Burman f.) Stapf & C. E. Hubb., malate type (NADP-me); *Panicum* (= *Urochloa*) *maximum* Jacq., aspartate type (PEP-ck); *Panicum miliaceum* L., aspartate type (NAD-me).]
- HATTERSLEY, P. W. Characterization of C₄ type leaf anatomy in grasses (Poaceae). Mesophyll: bundle sheath area ratios. *Ann. Bot.* II. **53**: 163–179. 1984. [Mean primary carbon assimilation area (mesophyll) per vein and mean assimilation/reduction ratio greatest in C₃ grasses; mean photosynthetic carbon reduction area (parenchymatous bundle sheath) per vein in C₄ grasses greatest in NAD-me genera.]
- . Variations in photosynthetic pathway. Pp. 49–64 in T. R. SODERSTROM *et al.*, eds., *Grass systematics and evolution*. Washington, D.C. 1987.
- HEISER, C. B., & T. W. WHITAKER. Chromosome number, polyploidy, and growth habit in California weeds. *Am. Jour. Bot.* **35**: 179–186. 1948. [Counts in *Digitaria*, *Echinochloa*, *Paspalum*, *Setaria*.]
- HESLOP-HARRISON, J. Pollen-stigma interaction and cross-incompatibility in the grasses. *Science* **215**: 1358–1364. 1982.
- HITCHCOCK, A. S. Catalogue of the grasses of Cuba. *Contr. U.S. Natl. Herb.* **12**: 183–256. 1909. [Discussion of genera related to *Paspalum*, including description of *Reimarochloa*; emended description of *Alloteropsis*.]
- . The genera of grasses of the United States, with special reference to the economic species. *U.S. Dep. Agr. Bull.* **772**. 307 pp. 1920. (Revised by A. CHASE, 1936.) [Detailed discussion of typification of North American genera.]
- & A. CHASE. The North American species of *Panicum*. *Contr. U.S. Natl. Herb.* **15**: 1–396. 1910. [*Panicum* and its segregates discussed; *Panicum* monographed for North America.]
- & ———. Tropical North American species of *Panicum*. *Ibid.* **17**: 459–539. 1915. [116 species.]

- & ———. Manual of the grasses of the United States. ed. 2. U.S. Dep. Agr. Misc. Publ. 200. 1951. [Paniceae, 570–737.]
- HOLM, L., J. V. PANCHO, J. P. HERBERGER, & D. L. PLUCKNETT. A geographical atlas of world weeds. xlix + 391 pp. New York. 1979.
- HOSHINO, T., & G. DAVIDSE. Chromosome numbers of grasses (Poaceae) from southern Africa. I. Ann. Missouri Bot. Gard. **75**: 866–873. 1988. [Counts in *Alloteropsis*, *Antheophora*, *Brachiaria* (= *Urochloa*), *Digitaria*, *Echinochloa*, *Panicum*, *Paspalidium*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Urochloa*.]
- HSU, C.-C. The Paniceae (Gramineae) of Formosa. *Taiwania* **9**: 33–57. 1963. [Keys and descriptions; chromosome counts in *Alloteropsis*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Oplismenus*, *Panicum*, *Paspalum*, *Sacciolepis* and *Setaria* contributed by C.-C. CHEN.]
- . The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. Jour. Fac. Sci. Univ. Tokyo Bot. **9**: 43–150. 1965. [Thorough treatment of many character systems in relation to generic limits of *Panicum* and several allied genera and to the infrageneric classification of *Panicum*.]
- . A guide to the Taiwan grasses, with keys to subfamilies, tribes, genera, and species. *Taiwania* **16**: 199–341. 1971. [Paniceae, 272–302.]
- . Preliminary chromosome studies on the vascular plants of Taiwan. (V). Cytotaxonomy on some monocotyledons. *Ibid.* **17**: 48–65. 1972. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Eriochloa*, *Panicum*, *Paspalum*, *Setaria*.]
- HUGHES, D. K. The genus *Panicum* of the Flora Australiensis. Bull. Misc. Inf. Kew **1923**: 305–332. 1923. [New combinations and/or new species in *Brachiaria*, *Digitaria*, *Echinochloa*, *Ichnanthus*, *Leptoloma*, *Panicum*, *Paspalidium*, *Urochloa*, all of which had been included in *Panicum* by Bentham; *Alloteropsis* and *Paractaenum* Beauv. discussed.]
- HUNZIKER, J. H., & G. L. STEBBINS. Chromosomal evolution in the Gramineae. Pp. 179–187 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D.C. 1987.
- JAUHAR, P. P. Cytogenetics of pearl millet. Advances Agron. **34**: 407–479. 1981. [All aspects of the cytogenetics of this crop.]
- JAVURKOVÁ, V. In: Chromosome number reports. LXIX. Taxon **29**: 703–730. 1980. [Counts in *Digitaria*, *Setaria*.]
- JONES, S. B., & N. C. COILE. The distribution of the vascular flora of Georgia. 230 pp. Athens, Georgia. 1988. [Gramineae, 29–49; genera listed alphabetically; one record per county.]
- JORDAN, J. L., L. S. JORDAN, & C. M. JORDAN. Prominent spermoderm patterns of Poaceae. Bot. Mag. Tokyo **96**: 269–272. 1983. [Seed coat patterns of 60 genera and 118 species of grasses examined using scanning electron microscopy; incl. *Axonopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Panicum* (incl. *Urochloa*), *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Trichachne* (= *Digitaria*).]
- JOSHI, A. B., B. D. PATIL, & P. L. MANCHANDA. Chromosome numbers in some grasses. Curr. Sci. Bangalore **28**: 454, 455. 1959. [Counts in *Panicum* and *Pennisetum*.]
- KANETA, M., & N. SUGIYAMA. Identification of flavone compounds in eighteen Gramineae species. Agr. Biol. Chem. **37**: 2663–2665. 1973. [*Digitaria ciliaris* (as *D. adscendens*) produces tricetin and isoorientin; *Setaria glauca* produces isoorientin and luteolin 7-O-rutinoside.]
- KAWAMITSU, Y., W. AGATA, & S. MIURA. Effects of vapour pressure difference on CO₂ assimilation rate, leaf conductance and water use efficiency in grass species. Jour. Fac. Agr. Kyushu Univ. **31**: 1–10. 1987. [Higher water use

- efficiency under severe conditions in C₄ grasses; incl. *Brachiaria* (= *Urochloa*), *Cenchrus*, *Hymenachne*, *Panicum*, *Paspalum*, *Setaria*.]
- KELLOGG, E. A., & C. S. CAMPBELL. Phylogenetic analyses of the Gramineae. Pp. 310-322 in T. R. SODERSTROM *et al.*, eds., *Grass systematics and evolution*. Washington, D.C. 1987.
- KHOSLA, P. K., & P. N. MEHRA. In: IOPB chromosome number reports. XLII. *Taxon* 22: 647-654. 1973. [Counts in *Digitaria*, *Oplismenus*, *Panicum* (incl. *Urochloa*), *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Urochloa*.]
- & P. SINGH. In: IOPB chromosome number reports. XXXV. *Ibid.* 21: 161-166. 1972. [Counts in *Cenchrus*, *Digitaria*, *Oplismenus*, *Setaria*.]
- KORNET, D. J. Conventional and fundamental problems in the delimitation of genera from a phylogenetic point of view. *Acta Bot. Neerl.* 37: 527-529. 1988. [Philosophy of generic circumscription.]
- KOYAMA, T. Grasses of Japan and its neighboring regions: An identification manual. x + 570 pp. Tokyo. 1987. [Paniceae, 298-388.]
- KRISHNASWAMY, N. Untersuchungen zur Cytologie und Systematik der Gramineen. *Beih. Bot. Centralbl.* 60A: 1-56. 1940. [Chromosome counts in *Cenchrus*, *Panicum* (incl. *Digitaria*, *Echinochloa*, *Eriochloa*, *Setaria*), *Paspalum*, *Pennisetum*.]
- . Origin and distribution of cultivated plants of South Asia: millets. *Indian Jour. Genet. Pl. Breed.* 11: 67-74. 1951. [*Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*.]
- LAMSON-SCRIBNER, F. Useful and ornamental grasses. U.S. Dep. Agr. Div. Agrost. Bull. 3. 119 pp. 1896. [Large number of grasses, incl. many Paniceae, mentioned.]
- LARSEN, K. Cytological studies in vascular plants of Thailand. *Dansk Bot. Ark.* 20: 211-275. 1963. [Chromosome counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Oplismenus*, *Panicum*, *Paspalidium*, *Paspalum*, *Sacciolepis*, *Setaria*.]
- LELONG, M. G. Noteworthy monocots of Mobile and Baldwin counties, Alabama. *Sida* 13: 101-113. 1988. [*Amphicarpum Muhlenbergianum* (Schultes) Hitchc., *Panicum nudicaule* Vasey, *Paspalum conjugatum* Berg., *Setaria corrugata* (Ell.) Schultes, *S. Faberi* W. Herrm.]
- LÖVE, Å., & D. LÖVE. In: Chromosome number reports. LXXI. *Taxon* 30: 506-517. 1981. [Counts in *Panicum*, *Setaria*.]
- MACROBERTS, D. T. A documented checklist and atlas of the vascular flora of Louisiana. Pteridophyta, Gymnospermae, and Monocotyledoneae. Bull. Mus. Life Sci. Louisiana State Univ. Shreveport. 7. 1989. [Gramineae, 155-245; genera listed alphabetically; one dot per county; representative specimen citations and annotations on status.]
- MALIK, C. P., & T. N. MARY. In: IOPB chromosome number reports. XXVII. *Taxon* 19: 437-442. 1970. [Counts in *Alloteropsis*, *Brachiaria*, *Digitaria*, *Eriochloa*, *Paspalum*, *Urochloa*.]
- & R. C. TRIPATHI. In: IOPB chromosome number reports. XXVII. *Ibid.* 19: 437-442. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Echinochloa*, *Paspalidium*, *Paspalum*, *Setaria*, *Urochloa*.]
- MATTEN, S. R., & D. B. DICKINSON. Sugar profiles of seedlings of *Zea Mays* and several weedy panicoid grasses. *Phytochemistry* 25: 2123-2125. 1986. [Incl. *Setaria Faberi*, *Panicum miliaceum*, *Sorghum bicolor* (L.) Moench (Andropogoneae), all of which differ from maize in having lesser amounts of fructose, glucose, and sucrose in their tissues.]
- MCNEILL, J., & W. G. DORE. Taxonomic and nomenclatural notes on Ontario grasses. *Nat. Canad.* 103: 553-567. 1976. [New combinations and discussions of nomenclatural problems in *Echinochloa*, *Panicum*, and *Setaria*.]

- MEHRA, P. N., & J. D. CHAUDHARY. In: IOPB chromosome number reports. XLVI. *Taxon* **23**: 801-812. 1974. [Counts in *Axonopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Hymenachne*, *Oplismenus*, *Panicum*, *Paspalum*, *Sacciolepis*.]
- & ———. In: IOPB chromosome number reports. XLIX. *Ibid.* **24**: 501-516. 1975. [Counts in *Digitaria*, *Echinochloa*, *Oplismenus*, *Panicum*, *Paspalum*, *Setaria*.]
- & ———. In: IOPB chromosome number reports. LIV. *Ibid.* **25**: 631-649. 1976. [Counts in *Alloteropsis*, *Axonopus*, *Brachiaria* (= *Urochloa*), *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Sacciolepis*.]
- & M. L. SHARMA. In: IOPB chromosome number reports. XXXIX. *Ibid.* **22**: 115-118. 1973. [Counts in *Digitaria*, *Oplismenus*, *Paspalum*, *Pennisetum*.]
- & ———. In: IOPB chromosome number reports. XLIX. *Ibid.* **24**: 501-516. 1975. [Counts in *Brachiaria*, *Paspalum*.]
- METCALFE, C. R. Gramineae. *Anat. Monocot.* **1**. lxi + 731. 1960.
- MITRA, K., & N. DATTA. In: IOPB chromosome number reports. XIII. *Taxon* **16**: 445-461. 1967. [Counts in *Eriochloa*, *Oplismenus*, *Paspalidium*, *Pennisetum*, *Setaria*, *Urochloa*.]
- MOFFETT, A. A., & R. HURCOMBE. Chromosome numbers of South African grasses. *Heredity* **3**: 369-373. 1949. [Counts in *Cenchrus*, *Digitaria*, *Panicum* (= *Urochloa*, in this case), *Rhynchelytrum* (= *Melinis*).]
- MORTON, J. F. Atlas of medicinal plants of Middle America. Bahamas to Yucatan. xxviii + 1420 pp. Springfield, Illinois. 1981. [Incl. *Digitaria*, *Echinochloa*, *Eriochloa*, *Lasiacis*, *Oplismenus*, *Panicum* (incl. *Urochloa*), *Paspalum*, *Pennisetum*.]
- MUNIYAMMA, M. In: IOPB chromosome number reports. LI. *Taxon* **25**: 155-164. 1976. [Counts in *Brachiaria* (= *Urochloa*), *Echinochloa*, *Melinis*.]
- & K. N. NARAYAN. In: IOPB chromosome number reports. XLVIII. *Ibid.* **24**: 367-372. 1975. [Counts in *Brachiaria* (= *Urochloa*), *Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum*.]
- , A. N. R. SINDHE, & K. N. NARAYAN. In: IOPB chromosome number reports. LII. *Ibid.* **25**: 341-346. 1976. [Counts in *Alloteropsis*, *Axonopus*, *Digitaria*, *Sacciolepis*.]
- MYERS, W. M. Cytology and genetics of forage grasses. *Bot. Rev.* **13**: 319-421. 1947. [Extensive bibliography through 1944.]
- NARAYAN, K. N., & M. MUNIYAMMA. In: IOPB chromosome number reports. XXXVIII. *Taxon* **21**: 679-684. 1972. [Counts in *Brachiaria* (= *Urochloa*), *Oplismenus*, *Pennisetum*.]
- NASH, G. V. Poaceae. Pp. 48-161 in J. K. SMALL, Flora of the southeastern United States. 1903. [Nine informal subdivisions of *Panicum*; *Phanopyrum* and *Steinchisma* distinct from *Panicum*; *Cenchropsis* described to accommodate *C. myosuroides* (Kunth) Nash (= *Cenchrus myosuroides* Kunth).]
- . Poaceae (Tribe Andropogoneae, *Arthraxon-Themeda*; Tribe Zoysieae; Tribe Tristegineae; Tribe Paniceae, *Leptocoryphium-Paspalum*, in part). *N. Am. Flora* **17**: 99-196. 1912. [Tristegineae (= subtribe Melinidineae), 142-144; Paniceae, 144-196.]; Poaceae (Tribe Paniceae, *Paspalum*, continued-*Panicum*, in part). *Ibid.* 197-288. 1915. [*Paspalum* by NASH; *Panicum* by A. S. HITCHCOCK.]; Poaceae (Tribe Paniceae, *Panicum*, continued-*Mniochloa*). *Ibid.* 289-354. 1931. [By A. S. HITCHCOCK.]
- . Gramineae. Pp. 107-295 in N. L. BRITTON & A. BROWN, An illustrated flora of the northern United States, Canada and the British Possessions, ed. 2. Vol. 1. Ophioglossaceae to Polygonaceae. Ferns to Buckwheat. 1913. [Type species designated for all genera occurring in the Illustrated Flora region.]
- NATH, J., M. S. SWAMINATHAN, & K. L. MEHRA. Cytological studies in the tribe Paniceae, Gramineae. *Cytologia* **35**: 111-131. 1970. [Chromosome counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Eriochloa*, *Panicum*, *Paspalum*,

Pennisetum, *Urochloa*; meiotic irregularities (univalents, laggards) in at least a few species of most of these genera.]

- NIELSEN, E. L. Grass studies. III. Additional somatic chromosome complements. *Am. Jour. Bot.* **26**: 366-372. 1939. [Counts in *Panicum*, *Paspalum*, and *Urochloa* (*Panicum teranum*) from Arkansas and Texas.]
- NUÑEZ, O. Investigaciones cariosistematicas en las gramíneas Argentinas de la tribus "Paniceae." *Revista Fac. Agron. Univ. Nac. La Plata* **28**: 229-256. 1952. [Numerous chromosome counts and cytological observations in *Axonopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Lasiacis*, *Leptocoryphium* (= *Anthaenantia*), *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*, *Stenotaphrum*, *Trichachne* (= *Digitaria*).]
- OHWI, J. Gramina Japonica. III. *Acta Phytotax. Geobot.* **11**: 27-56. 1942. [Many new combinations in *Digitaria*, *Echinochloa*, *Eriochloa*, *Paspalidium*, *Setaria*; sections and/or series established for *Digitaria*, *Eriochloa*, *Setaria*.]
- OLORODE, O. Chromosome counts in some Nigerian grasses. *Cytologia* **39**: 429-435. 1974. [Counts in *Brachiaria* (= *Urochloa*), *Digitaria*, *Echinochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*.]
- ONO, H., & T. TATEOKA. Karyotaxonomy in Poaceae. I. Chromosome and taxonomic relations in some Japanese grasses. *Bot. Mag. Tokyo* **66**: 18-27. 1953. [Chromosome counts in *Digitaria*, *Paspalum*, *Pennisetum*, *Sacciolepis*, *Setaria*.]
- PALISOT DE BEAUVOIS, A. M. F. J. *Essai d'une nouvelle agrostographie*. Paris. 1812. [*Anthaenantia*, *Axonopus*, *Echinochloa*, *Hymenachne*, *Melinis*, *Setaria*, *Urochloa* first described.]
- PARFITT, B. D., & N. A. HARRIMAN. In: Chromosome number reports. LXXI. *Taxon* **30**: 506-517. 1981. [Counts in *Digitaria*, *Panicum*.]
- PARODI, L. R. *Gramineas Bonariensis*. 4th ed. 112 pp. Buenos Aires. 1946. [Illustrations, keys, subfamilial and tribal alignments of Argentinian grasses; new chromosome counts in *Axonopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Lasiacis*, *Panicum*, *Paspalidium*, *Paspalum*, *Pennisetum*, *Setaria*, *Stenotaphrum* (many of the counts made by O. NUÑEZ).]
- & E. G. NICORA. Estudios sistemáticos sobre las Gramíneas—Paniceae argentinas y uruguayas. *Darwiniana* **15**: 65-111. 1969. [PARODI was a posthumous author of this paper; review of species in the smaller genera; *Panicum*, *Paspalum*, *Setaria* not included, except for one new species each in the first two genera.]
- PATTON, J. E., & W. S. JUDD. A phenological study of 20 vascular plant species occurring on the Paynes Prairie Basin, Alachua County, Florida. *Castanea* **53**: 149-163. 1988. [Incl. *Axonopus affinis*, *Panicum hemitomom*, *Paspalum notatum*.]
- PILGER, R. Bemerkungen zu *Panicum* und verwandten Gattungen. *Notizbl. Bot. Gart. Berlin* **11**: 237-247. 1931. [Eight subgenera in *Panicum*; 11 sections in subg. *Panicum*.]
- Gramineae. III. Unterfamilie Panicoideae. *Nat. Pflanzenfam.*, ed. 2. **14c**: 1-208. 1940. [Hierarchical classification of the subfamily, including infrageneric divisions; many new combinations and names for suprageneric taxa, but several lack cited basionyms.]
- Das System der Gramineae unter Ausschluss der Bambusoideae. *Bot. Jahrb.* **76**: 281-384. 1954. [Posthumous; hierarchical classification of the family.]
- PLATZER, H. Untersuchungen über die phänotypische und karyotypische Variabilität der europäischen Unkrauthirsens aus den Gattungen *Setaria*, *Digitaria* und *Echinochloa*. *Zeitschr. Pflanzenz.* **47**: 330-368. 1962. [Studies of phenotypic and karyotypic variability in wild millets.]
- FOHL, R. W. A taxonomic study on the grasses of Pennsylvania. *Am. Midl. Nat.* **38**: 513-600. 1947.

- . New species of *Digitaria*, *Pennisetum*, and *Poa* (Gramineae) from Costa Rica. *Fieldiana Bot.* **38**(2): 5–13. 1976.
- . Gramineae. In: *Flora Costaricensis. Ibid.* II. **4**: 1–608. 1980. [Excellent treatment; many species illustrated; useful comments on intergeneric relationships.]
- & G. DAVIDSE. Chromosome numbers of Costa Rican grasses. *Brittonia* **23**: 293–324. 1971. [Counts in *Antheophora*, *Axonopus*, *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Hymenachne*, *Oplismenus*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Sacciolepis*, *Setaria*, *Stenotaphrum*, *Trichachne* (= *Digitaria*).]
- & N. R. LERSTEN. Stem aerenchyma as a character separating *Hymenachne* and *Sacciolepis* (Gramineae, Panicoideae). *Brittonia* **27**: 223–227. 1975. [In addition to the saccate distal glume of *Sacciolepis*, presence of stem aerenchyma and leaf epidermal prickle hairs separate *Hymenachne* from *Sacciolepis*.]
- PRAT, H. La systématique des Graminées. *Ann. Sci. Nat. Bot.* X. **18**: 169–258. 1936. [Silica cells, microhairs, macrohairs, leaf anatomy, cytology, seedling leaves, embryos, caryopses, inflorescence morphology, and chemistry used to define three major lineages (panicoids, chloridoids, festucoids) arising from bambusoids.]
- . Vers une classification naturelle des Graminées. *Bull. Soc. Bot. France* **107**: 32–79. 1960. [Modern, synthetic treatment of the Gramineae at the subfamilial and tribal levels.]
- PRENDERGAST, H. D. V., & P. W. HATTERSLEY. Australian C₄ grasses (Poaceae): leaf anatomical features in relation to C₄ acid decarboxylation types. *Austral. Jour. Bot.* **35**: 355–382. 1987. [Incl. *Alloteropsis*, *Axonopus*, *Brachiaria* (incl. *Urochloa*), *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Melinis*, *Panicum* (incl. *Urochloa*), *Paspalidium*, *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Stenotaphrum*, *Urochloa*.]
- , ——— & N. E. STONE. New structural/biochemical associations in leaf blades of C₄ grasses (Poaceae). *Austral. Jour. Pl. Physiol.* **14**: 403–420. 1987. [*Alloteropsis semialata* (R. Br.) Hitchc. is the first recorded single-sheath species with PEP-ck biochemical pathway; other genera include *Melinis* (incl. *Rhynchelytrum*), *Panicum* (incl. *Urochloa*).]
- PRITCHARD, A. J. Meiosis and embryo sac development in *Urochloa mosambicensis* and three *Paspalum* species. *Austral. Jour. Agr. Res.* **21**: 649–652. 1970. [Four-nucleate aposporous embryo sacs in *U. mosambicensis*; 8-nucleate aposporous embryo sacs in *Paspalum* spp.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Gramineae by RADFORD; Paniceae, 125–159.]
- RAMAKRISHNAN, P. S., & A. K. KHOSLA. Seed dormancy in *Digitaria adscendens* (H.B.K.) Henr. and *Echinochloa colona* Link with a particular reference to covering structures. *Trop. Ecol. India* **12**: 112–122. 1971. [Both species have water-soluble germination inhibitors in their seed coats.]
- RAMAN, V. S., P. CHANDRASEKHARAN, & D. KRISHNASWAMI. Note on some chromosome numbers in Gramineae. *Curr. Sci. Bangalore* **28**: 127, 128. 1959a. [Counts in *Panicum* (= *Urochloa*, in this case), *Pennisetum*, *Stenotaphrum*.]
- , ——— & ———. Chromosome numbers in Gramineae. *Ibid.*: 453, 454. 1959b. [Counts in *Digitaria*, *Eriochloa*, *Paspalidium*, *Setaria*, *Urochloa*.]
- RAO, P. N., & L. B. MWASUMBI. In: Chromosome number reports. LXXI. *Taxon* **30**: 68–80. 1981. [Counts in *Cenchrus*, *Digitaria*, *Echinochloa*, *Panicum* (= *Urochloa*), *Paspalidium*, *Paspalum*, *Sacciolepis*, *Setaria*, *Stenotaphrum*.]
- RAU, N. S. On the chromosome numbers of some cultivated plants of South India. *Jour. Indian Bot. Soc.* **8**: 126–128. 1929. [Counts in *Echinochloa*, *Panicum*, *Pennisetum*.]

- REEDER, J. R. The embryo in grass systematics. *Am. Jour. Bot.* **44**: 756-768. 1957. [Illustrations of embryos of *Panicum clandestinum* L., *Rhynchelytrum roseum* (Nees) Stapf & C. E. Hubb. ex Bews (= *Melinis repens* (Willd.) Zizka), *Cenchrus pauciflorus* Benth., *Antheophora hermaphrodita* (L.) Kuntze.]
- . Notes on Mexican grasses. VI. Miscellaneous chromosome numbers. *Bull. Torrey Bot. Club* **94**: 1-17. 1967. [Counts in *Antheophora*, *Brachiaria* (= *Urochloa*), *Digitaria*, *Lasiacis*, *Oplismenus*.]; 2. *Ibid.* **95**: 69-86. 1968. [Counts in *Cenchrus*, *Digitaria*, *Echinochloa*, *Lasiacis*, *Oplismenus*, *Panicum*, *Paspalum*.]
- . In: Chromosome number reports. LXXXII. *Taxon* **33**: 126-134. 1984. [Counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Eriochloa*, *Lasiacis*, *Panicum*, *Paspalum*, *Pennisetum*, *Urochloa*.]
- & T. R. SODERSTROM. In: IOPB chromosome number reports. XVI. *Ibid.* **17**: 199-204. 1968. [Counts in *Echinochloa*, *Setaria*.]
- RENVOIZE, S. A. The grasses of Bahia. Royal Botanic Gardens, Kew. 301 pp. 1984. [Thorough treatment; illustrated.]
- RISCH, S. J., & C. R. CARROLL. Effects of seed predation by a tropical ant on competition among weeds. *Ecology* **67**: 1319-1327. 1986. [Ants harvest seeds in a frequency-dependent manner; plants studied include *Paspalum distichum* L., *Panicum clandestinum* L., and *Cenchrus ciliaris* L.; *Paspalum* preferred over *Daucus Carota* L.; *Panicum* preferred over *Cenchrus*.]
- RIVERA-BRENES, L., A. RODRÍGUEZ-CABRERA, & H. CESTERO. Comparison of giant pangola, signal grass, and common pangola as pasture crops in the mountain region of Puerto Rico. *Jour. Agr. Univ. Puerto Rico* **51**: 193-200. 1967. [*Digitaria* spp. and *Brachiaria* (= *Urochloa*) *brizantha*.]
- ROHWEDER, H. Versuch zur Erfassung der mengenmässigen Bedeckung des Darss und Zingst mit polyploiden Pflanzen. Ein Beitrag zur Bedeutung der Polyploidie bei der Eroberung neuer Lebensräume. *Planta* **27**: 501-549. 1937. [Chromosome counts in *Panicum* (= *Echinochloa*), *Setaria*.]
- ROSENKRANZ, E. Grasses native or adventive to the United States as new hosts of maize dwarf mosaic and sugarcane mosaic viruses. *Phytopathology* **68**: 175-179. 1978. [Incl. *Brachiaria* (incl. *Urochloa*), *Digitaria*, *Echinochloa*, *Eriochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Trichachne* (= *Digitaria*).]
- ROSHEVITS, R. Y. Zlaki: Vvedenie v izuchenie kormovykh i khlebynykh zlakov. Leningrad. 1937. (Grasses: An introduction to the study of fodder and cereal grasses. English translation by the Indian National Scientific Documentation Centre. vi + 635 pp. New Delhi. 1980.) [Keys, illustrations, descriptions, and discussions of the world's grasses, with emphasis on the economic importance of grasses in USSR.]
- SÁNCHEZ, E., & M. I. CASABONA. Presencia de cristales en hojas de Paniceae (Gramineae). *Bol. Soc. Argent. Bot.* **20**: 83-90. 1981. [Calcium oxalate crystals in mesophyll cells in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Digitaria*, *Eriochloa*, *Leptocoryphium* (= *Anthaenanthia*), *Oplismenus*, *Panicum*, *Paspalum*, *Pennisetum*, *Setaria*, *Stenotaphrum*, and other grasses.]
- SARKAR, A. K., M. CHAKRABORTY, N. C. SAHA, & S. K. DAS. In: IOPB chromosome number reports. LIV. *Taxon* **25**: 631-649. 1976. [Counts in *Digitaria*, *Panicum*, *Paspalum*, *Setaria*.]
- , M. CHAKRAVERTY, S. K. DAS, C. R. PAL, & D. HAZARA. In: Chromosome number reports. LXVII. *Ibid.* **29**: 347-367. 1980. [Counts in *Brachiaria* (= *Urochloa*), *Paspalum*, *Stenotaphrum*.]
- SAVILLE, D. B. O. Use of rust fungi (Uredinales) in determining ages and relationships in Poaceae. Pp. 168-178 in T. R. SODERSTROM *et al.*, eds., *Grass systematics and evolution*. Washington, D.C. 1987. [Paniceae more recently evolved than Andropogoneae; most rusts (*Puccinia* spp.) on Paniceae have diverged considerably from the ancestral morphology; treats these two tribes as subfamilies (Panicoideae and Andropogonoideae).]

- SAXENA, B. K., & B. K. GUPTA. In: IOPB chromosome number reports. XXVII. Taxon 19: 437-442. 1970. [Counts in *Brachiaria* (= *Urochloa*), *Digitaria*, *Oplismenus*, *Paspalidium*, *Paspalum*, *Setaria*, *Urochloa*.]
- SCHUSTER, J. Über die Morphologie der Grasblüte. Flora 100: 213-266. 1910. [Basic grass flower thought to be hexamerous; grass pistil tricarpellate; floral diagrams for *Digitaria*, *Paspalum*, *Pennisetum*.]
- SHANTHAMMA, C., K. N. NARAYAN, & A. SHUKUR. In: IOPB chromosome number reports. LII. Taxon 25: 341-346. 1976. [Counts in *Cenchrus*, *Eriochloa*, *Paspalidium*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*.]
- SHARMA, A. K., & D. N. DE. Cytology of some of the millets. Caryologia 8: 294-308. 1956. [Chromosome counts and karyotypes for species of *Setaria* and *Pennisetum*; *P. typhoideum* sometimes has abnormal meiosis, with early disjunction, non-disjunction, laggards.]
- SHARMA, M. L., & P. KUMAR. In: Chromosome number reports. LXIX. Taxon 29: 703-730. 1980. [Counts in *Digitaria*, *Oplismenus*, *Pennisetum*.]
- SHINNERS, L. H. Notes on Wisconsin grasses—IV. *Leptoloma* and *Panicum*. Am. Midl. Nat. 32: 164-180. 1944.
- . Notes on North Texas grasses. Rhodora 56: 25-38. 1954. [New species and combinations in *Paspalum*, *Echinochloa*; segregates of *Panicum capillare* lumped; key to *Cenchrus longispinus* complex.]
- SIDHU, M., & M. K. AHLUWALIA. Pollen studies in grass weeds of Punjab Plains, India. New Botanist 15: 39-50. 1988. [Key to pollen grains; all species monoporate except *Oplismenus Burmannii*, which was 1,2-zonoporate; all with faintly reticulate exine except *Paspalidium flavidum*, which was psilate.]
- SILVEUS, W. A. Grasses: Classification and description of species of *Paspalum* and *Panicum* in the United States. x + 526 pp. San Antonio, Texas. 1942.
- SIMON, B. K. A revision of the genus *Sacciolepis* (Gramineae) in the 'Flora Zambesiaca' area. Kew Bull. 27: 387-406. 1972. [*Sacciolepis* revised for southern Africa; incl. notes and a key dealing with several related genera (*Hymenachne*, *Panicum*, *Setaria*).]
- SINDHE, A. N. R., K. N. NARAYAN, & M. MUNIYAMMA. In: IOPB chromosome number reports. XLVIII. Taxon 24: 367-372. 1975. [Counts in *Echinochloa*, *Hymenachne*, *Paspalum*, *Paspalidium*.]
- SINGH, D. N., & M. B. E. GODWARD. Cytological studies in the Gramineae. Heredity 15: 193-199. 1960. [Cytological abnormalities in *Paspalum dilatatum* Poiret, including variable chromosome numbers within the same root tip, univalents and laggards at meiosis, and twin embryos; chromosome counts in *Brachiaria* (= *Urochloa*), *Cenchrus*, *Echinochloa*, *Eriochloa*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum* (= *Melinis*), *Setaria*.]
- SKOUSEN, J. G., & C. A. CALL. Grass and forb species for revegetation of mixed soil-lignite overburden in east central Texas. Jour. Soil Water Conserv. 42: 438-442. 1987. [*Cenchrus ciliaris*, *Panicum coloratum*, *P. virgatum*.]
- SMITH, E. B. An atlas and annotated list of the vascular plants of Arkansas. 2nd ed. iv + 489 pp. Fayetteville, Arkansas. 1988. [Gramineae, 336-380; genera arranged alphabetically; one dot per county; commentary, incl. status and miscellaneous data.]
- SODERSTROM, T. R., K. W. HILU, C. S. CAMPBELL, & M. E. BARKWORTH, eds. Grass systematics and evolution. xiv + 473 pp. Washington, D.C. 1987. [Information on all aspects of modern grass systematics.]
- SOHNS, E. R. *Cenchrus* and *Pennisetum*: fascicle morphology. Jour. Wash. Acad. Sci. 45: 135-143. 1955. [Generic limits indistinct, but *Pennisetum* characterized by prolonged sterile axis in spikelet fascicle, whereas *Cenchrus* has terminal spikelets.]
- SPRAGUE, T. A., J. RAMSBOTTOM, A. J. WILMOTT, & E. M. WAKEFIELD. International Botanical Congress, Cambridge, England, 1930. Nomenclature. Proposals by British botanists. 203 pp. London. 1929. [List of proposed conserved

- generic names, incl. *Setaria*, by SPRAGUE; proposed type species for Linnaean genera, incl. *Cenchrus* and *Panicum*, by A. S. HITCHCOCK & M. L. GREEN.]
- STAFF, O. Gramineae. Tribe Paniceae. Pp. 423-1072 in *Flora of tropical Africa*. Vol. 9. 1919-1934. [Thorough treatment of African grasses, with many innovations, realignments, discussions of problems; pp. 769-1072 co-authored by C. E. HUBBARD.]
- STEBBINS, G. L. Cytogenetics and evolution of the grass family. *Am. Jour. Bot.* **43**: 890-905. 1956. [Overview of relationships; description of hypothetical original grasses; discussion of role of hybridization and polyploidy in grass evolution.]
- TAIRA, H. Studies on amino acid contents in plant seeds. III. Amino acid contained in the seed of Gramineae (Part 2). (In Japanese; English summary.) *Bot. Mag. Tokyo* **76**: 340, 341. 1966. [Subfamily Panicoideae high in alanine and leucine, low in lysine and arginine.]
- TATEOKA, T. Karyotaxonomic studies in Poaceae, I. *Ann. Rep. Natl. Inst. Genet. Japan* **4**: 45-47. 1954. [Chromosome counts in *Echinochloa*, *Panicum*, *Setaria*.]; II. *Ibid.* **5**: 68, 69. 1955. [Counts in *Cenchrus*, *Digitaria*, *Oplismenus*, *Paspalum*, *Pennisetum*, *Setaria*.]; III. *Ibid.* **6**: 73, 74. 1956a. [Counts in *Oplismenus*, *Panicum*, *Paspalum*, *Setaria*.]; IV. Chromosomes and systematic relationships of several species. *Bot. Mag. Tokyo* **69**: 112-117. 1956b. [Counts in *Oplismenus*, *Panicum*, *Paspalum*, *Setaria*.]
- . Reexamination of anatomical characteristics of the leaves in Eragrostoideae and Panicoideae (Poaceae). (In Japanese; English summary.) *Jour. Jap. Bot.* **31**: 210-218. 1956c. [Many genera characterized.]
- . A cytological study of some Mexican grasses. *Bull. Torrey Bot. Club* **89**: 77-82. 1962. [Chromosome counts in *Antheophora*, *Lasiacis*, *Panicum*, *Paspalum*, *Rhynchelytrum* (= *Melinis*), *Setaria*, *Trichachne* (= *Digitaria*).]
- . Chromosome numbers of some grasses from Madagascar. *Bot. Mag. Tokyo* **78**: 306-311. 1965a. [Counts in *Brachiaria* (= *Urochloa*), *Digitaria*, *Panicum*, *Paspalum*, *Pennisetum*, *Sacciolepis*, *Stenotaphrum*.]
- . Chromosome numbers of some East African grasses. *Am. Jour. Bot.* **52**: 864-869. 1965b. [Counts in *Alloteropsis*, *Digitaria*, *Echinochloa*, *Melinis* (incl. *Rhynchelytrum*), *Oplismenus*, *Panicum*, *Paspalidium*, *Paspalum*, *Pennisetum*, *Setaria*.]
- THOMASSON, J. R. Fossil grasses: 1820-1986 and beyond. Pp. 159-167 in T. R. SODERSTROM *et al.*, eds., *Grass systematics and evolution*. Washington, D.C. 1987.
- TISCHLER, G. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins, mit Ausblicken auf andere Floregebiete. *Bot. Jahrb.* **67**: 1-36. 1935. [Chromosome counts in *Panicum* (= *Echinochloa*, *Digitaria*), *Setaria*.]
- TROUIN, M. Nombres chromosomiques de quelques graminées du Soudan. *Adansonia* **12**: 619-624. 1972. [Counts in *Brachiaria* (= *Urochloa*), *Digitaria*, *Setaria*.]
- TSVELEV, N. N. Zlaki SSSR. Two parts. Leningrad. 1976. (Grasses of the Soviet Union. English translation by B. R. SHARMA. Two parts. 1196 pp. Rotterdam. 1984.) [Paniceae, 985-1032, in translation.]
- . The system of grasses (Poaceae) and their evolution. *Bot. Rev.* **55**: 141-204. 1989. [Novel system with only two subfamilies recognized, Bambusoideae and Pooideae; probably less paraphyletic than other classification systems; however, relationships below the subfamilial level poorly resolved.]
- VASEY, G. Notes on grasses. The genus *Panicum* in the United States. *U.S. Dep. Agr. Bot. Bull.* **8**: 20-39. 1889. [Broad concept of *Panicum*, includes *Digitaria*, *Setaria*, *Urochloa*.]
- VOGEL, J. C., A. FULS, & A. DANIN. Geographical and environmental distribution of C₃ and C₄ grasses in the Sinai, Negev, and Judean deserts. *Oecologia* **70**: 258-265. 1986. [C₃ grasses have an adaptive advantage where low minimum

temperatures characterize winter growing season; C_4 grasses increase in importance with decreasing rainfall, and dominate areas where temperatures are high all year.]

- VOSS, E. G. Nomenclatural notes on monocots. *Rhodora* **68**: 435–463. 1966. [*Panicum*, *Paspalum*, *Setaria*.]
- WANG, S.-J., P.-C. CHAO, & J.-H. LI. The major types of caryopses of the Chinese Gramineae in relation to systematics. (In Chinese; English abstract.) *Acta Phytotax. Sinica* **24**: 327–345. 1986. [Descriptions of caryopses in nine genera represented in our area: *Digitaria*, *Echinochloa*, *Eriochloa*, *Oplismenus*, *Panicum*, *Paspalum*, *Pennisetum*, *Sacciolepis*, *Setaria*.]
- WATSON, L., & E. M. BELL. A surface-structural survey of some taxonomically diverse grass pollens. *Austral. Jour. Bot.* **23**: 981–990. 1975. [*Echinochloa*, *Paspalum*, *Pennisetum*.]
- , H. T. CLIFFORD, & M. J. DALLWITZ. The classification of Poaceae: subfamilies and supertribes. *Austral. Jour. Bot.* **33**: 433–484. 1985. [Distributed 720 currently recognized genera among five subfamilies and six supertribes; detailed descriptions.]
- & M. J. DALLWITZ. Grass genera of the world. Illustrations of characters, descriptions, classification, interactive identification, information retrieval. 45 pp. + microfiche + floppy disks. Canberra. 1988 (revised 1989).
- & C. R. JOHNSTON. Taxonomic variation in stomatal insertion among grass leaves. *Austral. Jour. Bot.* **26**: 235–238. 1978. [Most panicoids have guard cells flush against or overlapping adjacent epidermal cells.]
- WEBSTER, R. D. The Australian Paniceae (Poaceae). iii + 322 pp. Berlin. 1987. [45 genera; a thorough and useful treatment.]
- . Genera of the North American Paniceae (Poaceae: Panicoideae). *Syst. Bot.* **13**: 576–609. 1988. [25 genera recognized.]
- , J. H. KIRKBRIDE, & J. V. REYNA. New World genera of the Paniceae (Poaceae: Panicoideae). *Sida* **13**: 393–417. 1989. [Key and descriptions for 50 genera.]
- & J. V. REYNA. Genera of Mesoamerican Paniceae (Poaceae: Panicoideae). *Ibid.* 187–221. 1988. [Keys to all genera in the area; detailed descriptions and discussions of genera not found in North America.]
- WUNDERLIN, R. P. Guide to the vascular plants of Central Florida. 472 pp. Tampa, Florida. 1982. [Gramineae, 51–96; genera arranged alphabetically.]
- , B. F. HANSEN, & D. W. HALL. The vascular flora of Central Florida: taxonomic and nomenclatural changes, additional taxa. *Sida* **11**: 232–244. 1985. [*Eriochloa Michauxii* (Poir.) Hitchc. var. *Simpsonii* Hitchc., *Paspalum Nicorae* Parodi, *Setaria italica* (L.) Beauv. recorded.]; II. *Ibid.* **13**: 83–91. 1988. [Typification of *Paspalum distichum* L. discussed; *Digitaria bicornis* (Lam.) Roemer & Schultes ex Loudon new to the area.]
- YEOH, H.-H., & L. WATSON. Systematic variation in amino acid compositions of grass caryopses. *Phytochemistry* **20**: 1041–1051. 1981. [Characteristic amino acid profile for the Paniceae, regardless of photosynthetic pathway; Paniceae intermediate between Chloridoideae and Andropogoneae, but most similar to the latter in amino acid constitution.]
- ZIZKA, G. Revision der Melinideae Hitchcock (Poaceae, Panicoideae). *Bibliot. Bot.* **138**: 1–149. 1988. [Recognizes *Tricholaena* Schrader ex Schultes and *Melinis* Beauv., but merges *Rhynchelytrum* Nees with *Melinis*.]
- ZULOAGA, F. O., & T. R. SODERSTROM. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). *Smithson. Contr. Bot.* **59**. iv + 63 pp. 1985. [Species formerly included in *Panicum* assigned to *Brachiaria*, *Homolepis* Chase, *Ichnanthus* Beauv., *Paspalum*, *Streptostachys* Desv. emend. Zuloaga & Soderstrom, and *Tatianyx* Zuloaga & Soderstrom.]

KEY TO THE GENERA OF TRIBE PANICEAE (GRAMINEAE) IN THE
SOUTHEASTERN UNITED STATES.

General characters: *Perennials or annuals; stems unbranched or branched; leaves with kranz or non-kranz anatomy, rarely with transverse veins connecting longitudinal veins; leaf blades linear to ovate, generally cordate to cuneate at base; inflorescences paniculate, usually terminal, open or contracted, often with racemose, digitate, solitary, or further reduced branches; spikelets 2 flowered, usually dorsiventrally compressed, sometimes terete or laterally compressed, usually disarticulating below the glumes; proximal floret staminate or sterile, with or without palea; distal floret perfect, paleate; glumes 1 or 2 (0 in one genus), upper glume often as long as spikelet; lemmas membranaceous or hardened, distal lemma (and palea) often indurate; stamens 3 (2).*

- A. Spikelets, or clusters of spikelets, subtended by one to several conspicuous bristles, spines, or hardened dilated bracts.
 - B. Disarticulation occurring between each spikelet and its pedicel, spikelets therefore falling independent of bristle or fascicle of bristles 19. *Setaria*.
 - B. Disarticulation occurring below the spikelet-bristle (-bract) unit, spikelets therefore falling with the bristles, spines, or dilated bracts.
 - C. Cluster of 4 spikelets surrounded by 4 hardened dilated bracts, inflorescence spiciform 5. *Antheophora*.
 - C. Clusters of 1-6 spikelets subtended by a fascicle of bristles or spines.
 - D. Clusters of spikelets enclosed or subtended by bur-like series of spines and bristles that are fused at least near the base 4. *Cenchrus*.
 - D. Clusters of spikelets subtended by groups of bristles that are free to the base 3. *Pennisetum*.
- A. Spikelets single, paired, or in threes, not all subtended or enclosed by bristles, spines, or bracts.
 - E. Margins of distal lemma flat, membranaceous, thinner than body.
 - F. Distal lemma awned; proximal glume awned 13. *Alloteropsis*.
 - F. Distal lemma acute or acuminate, not awned; proximal lemma absent or acute to obtuse, not awned.
 - G. Spikelets embedded in rachis, and primary branches of inflorescence often embedded in main inflorescence axis; disarticulation at nodes of main inflorescence axis 21. *Stenotaphrum*.
 - G. Neither spikelets nor primary branches of inflorescence embedded in main inflorescence axis; disarticulation at base of spikelet.
 - H. Primary branches of inflorescence solitary, digitate, or racemose, with second, subsessile spikelets.
 - I. Spikelets adaxial, dorsal side of proximal lemma oriented toward rachis; proximal glume absent; internodes usually solid 18. *Axonopus*.
 - I. Spikelets abaxial, dorsal side of proximal lemma oriented away from rachis; proximal glume present or absent; internodes usually hollow 2. *Digitaria*.
 - H. Primary branches of inflorescence arranged in a panicle, not racemose; spikelets generally conspicuously pedicellate, not second.
 - J. Spikelets laterally compressed; apex of distal glume erose, lobed, or notched 22. *Melinis*.
 - J. Spikelets dorsiventrally compressed; apex of distal glume obtuse to acute, not irregular in outline.
 - K. Margins of distal lemma enclosing distal palea; distal lemma apex never differentiated; distal lemma indurate 2. *Digitaria*.

- K. Margins of distal lemma gaping, distal palea not enclosed at apex; distal lemma apex sometimes flared and hyaline; distal lemma papery1. *Anthraenantia*.
- E. Margins of distal lemma as thick and firm as rest of lemma.
 - L. Subterranean cleistogamous spikelets present, larger than spikelets of aerial inflorescence9. *Amphicarpum*.
 - L. Subterranean spikelets absent.
 - M. Apex of distal lemma with a tuft of white hairs; spikelets terete, black in fruit8. *Lasiacis*.
 - M. Apex of distal lemma glabrous; spikelets dorsiventrally or laterally compressed, not terete.
 - N. Spikelets laterally compressed; apex of distal glume erose, lobed, or notched22. *Melinis*.
 - N. Spikelets dorsiventrally compressed; apex of distal glume acute to obtuse or truncate, but not irregular in outline.
 - O. Distal glume saccate; inflorescence spiciform11. *Sacciolepis*.
 - O. Distal glume not saccate; inflorescence spiciform to diffuse.
 - P. Distal lemma and palea rugose.
 - Q. Branches of inflorescence terminating in a bristle.
 - R. Branches of inflorescence racemose, secund20. *Paspalidium*.
 - R. Branches of inflorescence arranged in a diffuse or contracted panicle, not secund19. *Setaria*.
 - Q. Branches of inflorescence terminating in a spikelet.
 - S. Proximal glume fused with callus at base of spikelet to form a cup-like or bead-like structure15. *Eriochloa*.
 - S. Proximal glume distinct, not fused with callus; no cup-like or bead-like structure at base of spikelet14. *Urochloa*.
 - P. Distal lemma and palea smooth to muricate.
 - T. Proximal glume encircling spikelet base.
 - U. Branches of inflorescence racemose, secund; apex of distal palea exposed (not fully enclosed by distal lemma); base of leaf blades incised12. *Echinochloa*.
 - U. Branches of inflorescence arranged in a panicle, not racemose; apex of distal palea enclosed by margins of distal lemma; base of leaf blades cuneate to rounded.
 - V. Margins of distal lemma flat10. *Hymenachne*.
 - V. Margins of distal lemma involute7. *Panicum*.
 - T. Proximal glume not encircling spikelet base.
 - W. Spikelets laterally compressed; stems slender, prostrate, creeping; proximal glume awned, awns viscid6. *Oplismenus*.
 - W. Spikelets dorsiventrally compressed, awnless; stems generally erect, although stolons may also be present.
 - X. Branches of inflorescence racemose.
 - Y. Both glumes absent; stamens 2; leaf sheaths with apical tuft of hairs; disarticulation at base of primary inflorescence branches17. *Reimarochloa*.
 - Y. At least one glume present; stamens 3; leaf sheaths glabrous or pubescent, but without apical tuft of hairs.
 - Z. Proximal glume present.
 - aa. Spikelets embedded in rachis, and primary branches often embedded in main inflorescence axis; disarticulation at nodes of main inflorescence axis21. *Stenotaphrum*.

- aa. Neither spikelets nor branches embedded; spikelets secund on rachis; disarticulation at base of spikelet.....16. *Paspalum*.
- Z. Proximal glume absent.
 - bb. Spikelets adaxial, dorsal side of proximal lemma oriented toward rachis; pedicel apex concave 18. *Axonopus*.
 - bb. Spikelets abaxial, dorsal side of proximal lemma oriented away from rachis; pedicel apex truncate or convex16. *Paspalum*.
- X. Branches of inflorescence arranged in a panicle or solitary.
 - cc. Spikelets secund on solitary, digitate, or alternating racemose branches of inflorescence; proximal glume usually absent; pedicel apex truncate or convex..... 16. *Paspalum*.
 - cc. Spikelets scattered on branches of an open panicle; proximal glume always present; pedicel apex concave 7. *Panicum*.

Subtribe DIGITARIINAE Butzin, Willdenowia 6: 509. 1972.

1. *Anthraenantia* Palisot de Beauvois, Essai Agrost. 48. 1812.⁵

Short-rhizomatous [caespitose] perennials. Stems erect, [30] 50–120 cm high, from non-tuberos [tuberos] bases; internodes spongy to hollow; nodes glabrous. Leaves mostly on lower half of stem; sheath margins glabrous to pubescent; ligule a short, fringed membrane; blades linear, flat, glabrous to scabrous, margins sometimes ciliate, truncate at base, sometimes disarticulating from sheaths; photosynthesis C₄, biochemical pathway unknown. Inflorescences paniculate, narrow, with erect to spreading primary branches and spreading secondary branches terminating in spikelets. Spikelets obovoid, laterally (dorsiventrally) compressed, disarticulating below the glume, pedicellate (pedicel apices cupuliform), solitary; proximal florets staminate [sterile], paleate [epaleate]. Calli undifferentiated. Glumes 1, equalling or slightly shorter than proximal lemmas, densely villous, hairs arranged in lines, acute [obtuse], 5–7 nerved (hairs and/or body of glume and proximal lemmas sometimes partly anthocyanic in *A. rufa*). Proximal lemmas equalling and less firm than distal lemmas, densely villous, hairs arranged in lines, awnless, 5 nerved; distal lemmas chartaceous to cartilaginous, glabrous, brown, dull, acute, 3–5 nerved, with flat margins thinner than body, with [without] conspicuous germination flap. Distal paleas chartaceous to cartilaginous, glabrous, awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red or brown. Caryopses (grains) dorsiventrally

⁵Palisot de Beauvois used three different spellings for this genus. Although Clayton & Renvoize note that *Anthenantia* is etymologically correct, *Anthraenantia* is the spelling used at the place of description in the text. This is the spelling that has been taken up by most authors.

compressed, smooth; pericarp thin; endosperm hard. Base chromosome number unknown. (Including *Leptocoryphium* Nees.) TYPE SPECIES: *Anthaenantia villosa* (Michx.) Beauv. (*Phalaris villosa* Michx.), the only species included in the genus at the time of its description. (Name from Greek *antheo*, to bloom, and *enantios*, opposite, in reference to the arrangement of staminate and perfect florets within the spikelet.) — SILKYSCALE.

A genus of three or four species occurring in dry to moist woodlands and along disturbed roadsides in the southeastern United States, Central America, and South America. The two North American species, *Anthaenantia rufa* (Ell.) Schultes, purple silkyscale (leaves narrow (3–5 mm wide) with margins scaberulous, spikelets purplish, long-pubescent), and *A. villosa*, green silkyscale (leaves broad (5–10 mm wide) with margins papillose-ciliate near base, spikelets green, short-pubescent), have very similar ranges (Florida northward on the Coastal Plain to central North Carolina, and west to eastern Texas). *Anthaenantia rufa* has also been found in southeastern Arkansas (E. Smith).

Virtually nothing is known about the biology of this genus. It is distinctive morphologically, but no one has examined its relationships closely. Similarities between *Anthaenantia* and *Leptocoryphium* led both Bentham and Webster (1988) to merge these genera under *Anthaenantia*. According to Watson & Dallwitz, the differences between them include only the structure of the proximal floret and minor anatomical features of the leaves, characters that often vary within panicoid genera. Butzin (1970) placed *Anthaenantia* in subtribe Otachyriinae Butzin, along with *Phanopyrum* and *Amphicarpum*. These two genera are close to *Panicum* (*Phanopyrum* is often merged with *Panicum*, as it is in this treatment), and there is little basis for assigning these genera to a subtribe distinct from the Setariinae (including Panicinae). Clayton & Renvoize placed *Anthaenantia* in subtribe Digitariinae Butzin, and Webster (1988) concluded that this genus is most similar to *Digitaria* sect. *Trichachne* (Nees) Stapf. However, problems in the delimitation of the three subtribes make them virtually useless taxonomically. Careful analyses are necessary to resolve the intergeneric relationships.

Davidse (1987) suggested that, due to the presence of prominent hairs on the spikelets, the propagules of species in this genus are dispersed by wind and/or adhesion.

REFERENCES:

Under references for tribe see BENTHAM; BLOMQUIST; BUTZIN (1970); CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1975); HALL; JONES & COILE; MACROBERTS; RADFORD *et al.*; E. SMITH; WATSON & DALLWITZ; WEBSTER (1988); and WUNDERLIN.

2. *Digitaria* Haller, Hist. Stirp. 2: 244. 1768, nom. cons.

Rhizomatous, stoloniferous, decumbent, or caespitose perennials or annuals. Stems 20–300 cm high; internodes hollow [solid]; nodes glabrous or pubescent. Leaf sheaths glabrous or pubescent; ligule a fringed or unfringed membrane; blades linear to lanceolate, flat or involute [folded], glabrous to scabrous or pubescent, with cuneate to rounded bases, rolled in bud; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences paniculate, open or contracted, with 1–many spike-like primary branches and appressed or spreading secondary branches terminating in spikelets (branches not spike-like in *D. cognata*), digitate or not [sometimes also with cleistogamous flowers]; rachides unwinged or winged, glabrous or pubescent. Spikelets solitary or in 2's or 3's, dorsiventrally compressed, disarticulating below the glumes (or the whole inflorescence disarticulating as a unit in *D. cognata*), abaxial, secund, pedicellate (pedicel apices truncate, discoid, or cupuliform); proximal florets staminate or neuter, paleate or epaleate; rachilla short or conspicuous between glumes. Calli undifferentiated. Glumes 1 or 2, unequal, glabrous or pubescent (pubescence glandular in several species), obtuse or acute; proximal glumes minute or absent, membranaceous, 0–1 nerved; distal glumes equalling or shorter than proximal lemmas, glabrous or pubescent, acute [with awn-like tip], [with gibbous pouch or spur at base], [1] 3–5 [7] nerved. Proximal lemmas glabrous to pubescent, acute, [3] 5–7 [9] nerved; distal lemmas equalling or slightly shorter than distal glumes, cartilaginous, glabrous, smooth, striate, or muricate, dull, acute to acuminate or mucronate, 1–3 nerved, with flat, thin margins and conspicuous germination flap. Distal paleas entire, 2 nerved, sometimes 2 keeled. Lodicules 2. Ovaries with styles fused or free, stigmas red. Caryopses (grains) smooth; pericarp thin; endosperm hard, without lipids, containing compound starch grains. Base chromosome number 9. (Including *Valota* Adanson, *Trichachne* Nees, *Syntherisma* Walter, *Leptoloma* Chase, *Digitariopsis* C. E. Hubbard, *Digitariella* de Winter.) TYPE SPECIES: *Digitaria sanguinalis* (L.) Scop., type cons., see ICBN, 1988. (Name from Latin, *digitatus*, having fingers, and suffix *-aria*, denoting a thing like, in reference to the arrangement of inflorescence branches in many species.) — CRABGRASS, FINGERGRASS, PANGOLA GRASS, SOURGRASS, WITCHGRASS, WITCHWEED.

A genus of about 220 species of dry or moist woods, natural and disturbed grasslands, moist riverbanks, dunes, and waste areas, distributed in tropical, subtropical, and temperate regions. About 25 species occur in North America, almost all of them in the southeastern United States. Most are adventive weeds. Henrard (1950) recognized four subgenera. *Solitaria* (Hackel) Henr., *Setariopsis* (Stapf) Henr., *Leptoloma* (Chase) Henr., and *Eudigitaria* (Stapf) Henr. (= *Digitaria*). The first three were not further subdivided, but Henrard (1950) recognized 32 sections within subg. *Digitaria*. His infrageneric classification relies on spikelet number (one, two, or more per group),

presence or absence of spikelet pedicels, inflorescence branching patterns, degree of development of the proximal glume, spikelet indumentum, perennation and growth habit, and fruit color, but the greatest emphasis was placed on indumentum. More recent students of *Digitaria* have found Henrard's sections to be too finely split (Clayton, 1974a; Clayton & Renvoize; Goetghebeur & van der Veken; Veldkamp; Webster, 1983), and Clayton & Renvoize question whether or not a reasonable infrageneric classification is possible at all. For that reason, it does not seem prudent to enumerate all of the southeastern species with reference to Henrard's (1950) scheme. However, a few of the subgroups are distinct and warrant mention.

Two of the four subgenera recognized by Henrard (1950) are represented by species occurring in North America. Subgenus *LEPTOLOMA* contains *D. cognata* (Schultes) Pilger, fall witchgrass, fall witchweed, $n = 18, 35, 36$, a caespitose perennial with a paniculate 'tumbleweed' inflorescence and short-pubescent spikelets. It is widespread in North America, occurring from New Hampshire, Ontario, and Minnesota south and west to northern Florida and Arizona. It is a plant of dry, open, sunny savannahs and prairies. All other North American species belong to subg. *DIGITARIA*. They fall within 10 of Henrard's (1950) sections. Sect. *TRICHACHNE* (Nees) Henr. was treated as a distinct genus by many early authors. Its species have well-developed proximal glumes that are somewhat separated from the distal glume and lemmas by a prolonged rachilla internode, and long-pilose spikelets. Included in this section are several southwestern American and South American species, as well as *D. insularis* (L.) Mez ex Ekman, sourgrass, silkygrass, $n = 18, 2n = 36$, the type species of the section, which occurs from central Florida and southern Texas southward to Central America and the West Indies.

Other sections within subg. *DIGITARIA* are poorly defined. Several of those sections are based on single characters that may reflect convergence and are undoubtedly polyphyletic (e.g., Clayton, 1974a).

Several species of the Southeast are in the *Digitaria sanguinalis* complex. All are annual weeds commonly known as crabgrasses. Chippindall, Ebinger (1962), Veldkamp, and Webster (1983) have helped to clarify the taxonomy of this complex. Six species occur in North America: *D. bicornis* (Lam.) R. & S., tropical crabgrass, $n = 36, 2n = 72$; *D. ciliaris* (Retz.) Koeler, southern crabgrass, $n = 9, 18, 27, 36, 2n = 36, 54, 70, 72$; *D. horizontalis* Willd., Jamaica crabgrass, $n = 9, 18, 27, 2n = 30, 36$; *D. nuda* Schum., $2n = 36$; *D. sanguinalis*, common crabgrass, $n = 14(?)$, $18, 27, 2n = 34, 36, 40, 44, 45, 48$), and *D. setigera* Roem. & Schultes, $n = 18, 27, 2n = 36$). *Digitaria sanguinalis* is the hardiest of them, occurring from southern Canada to northern Alabama, Louisiana, and Texas. The other five species occur mainly in the south (*D. horizontalis*, *D. nuda*, and *D. setigera* only in Florida), although *D. ciliaris* is found northward to Long Island.

Several species are endemic to Florida. *Digitaria albicoma* Swallen (spikelets glabrous, panicle with 5-9 branches), *D. pauciflora* Hitchc.

(spikelets glabrous, panicle with 2 or 3 branches, distal glume 3 nerved), *D. Simpsonii* Fern. (spikelets glabrous, panicles with 6–8 branches, distal glume 5 nerved), and *D. subcalva* Hitchc., Plant City fingergrass (spikelets appressed-pubescent, panicles with 2–4 branches) are perennials, and all have winged rachises, non-glandular straight pubescence (if any), and distal glumes and proximal lemmas of nearly equal length to each other and to the distal lemmas. *Digitaria dolichophylla* Henr. is very closely related to the widespread *D. filiformis* (L.) Koeler, slender crabgrass, $2n = 36$, but *D. dolichophylla* differs in having long, involute, setaceous, and curled leaves, and single or paired, erect racemes (vs. short, flat, straight leaves, and paired, divergent racemes). Both of these species, and *D. Ischaemum* (Schreber) Muhl., $2n = 36$, a widespread weed, have the spikelets covered with capitellate pubescence, but *D. Ischaemum* has a winged rachis, and *D. dolichophylla* and *D. filiformis* do not. *Digitaria leucocoma* (Nash) Urban has been separated from *D. filiformis* and *D. villosa* (Walter) Pers., shaggy crabgrass, by Henrard (1950) and others on the basis of slight differences in the lengths of distal and proximal lemmas, and in leaf-sheath pubescence. These characters are trivial, and Hitchcock and most other authors do not recognize *D. leucocoma* at any rank. *Digitaria floridana* Hitchc., Florida crabgrass, resembles *D. filiformis* in inflorescence structure, although its pubescence is eglandular. Both *D. floridana* and *D. Ischaemum* have a winged rachis. *Digitaria gracillima* (Scribner) Fern., longleaf fingergrass, has glabrous spikelets with short, obtuse distal glumes (proximal glumes absent), and 5-nerved proximal lemmas. *Digitaria Bakeri* Fern., with longer distal glumes, has occasionally been retained as a distinct species (e.g., Henrard, 1950; Nash, 1903), but most recent authors do not recognize it (Hitchcock & Chase, 1951; Hall).

Digitaria texana Hitchc. has been reported from two locations in Louisiana, but MacRoberts doubts the authenticity of these reports.

Other species have been brought to the Southeast, to test their efficacy as pasture grasses. Some of these have spread from cultivation and are naturalized. Several members of the *Digitaria eriantha* Steud. complex (stolons and/or rhizomes present, spikelets villous, proximal glumes well developed, bristles along margins of proximal lemmas often colored, rigid, and with tuberculate bases) have been cultivated in Florida, and a few of these (*D. decumbens* Stent, pangola grass, $2n = 27, 30$; *D. milaniana* (Rendle) Stapf, $n = 9, 2n = 18$, and *D. Pentzii* Stent, $2n = 18, 27, 36, 54$) have become naturalized (Hall). Other taxa⁶ have entered the continent and persist as weeds. Webster & Shaw considered the relationships between the perennial species (sect. *Erianthae*) and the annuals of sect. *Digitaria*, and concluded that the two sections

⁶Taxonomists differ greatly in the treatment of taxa in sect. *Erianthae* Henr. Numerous species have been recognized by Henrard, Chippindall, and others, but recently Kok (1984) has submerged many of the segregates into *D. eriantha*.

should be maintained on the basis of perennation, pubescence patterns, and leaf anatomy.

Clayton & Renvoize put *Digitaria* in subtribe Digitariinae, and Tsvelev (1976) placed it in the somewhat more inclusive subtribe Brachiariinae Butzin. Most other genera in Clayton & Renvoize's subtribe Digitariinae are monotypic or are small genera of Africa or Australia; the exception, *Anthaenantia* (incl. *Leptocoryphium*), contains species native to North America. Stapf felt that *Digitaria* was related to *Alloterospis*. Pohl (1980) believed that *Digitaria* was most closely related to *Reimarochloa* Hitchc., *Hymenachne* Beauv., and *Leptocoryphium* (= *Anthaenantia*). These views fit somewhere between those of Clayton & Renvoize and Watson & Dallwitz, whose phenetic analysis placed *Digitaria* close to *Stereochlaena* Hackel, *Tarigidia* Stent, *Echinochloa* Beauv., and *Reimarochloa*. *Anthaenantia*, *Stereochlaena*, and *Tarigidia* are in subtribe Digitariinae, but *Alloterospis*, *Echinochloa*, *Hymenachne*, and *Reimarochloa* are in subtribe Setariinae (Clayton & Renvoize). Phenetic analyses thus yield estimates of relationship that differ to some degree with those of the most recent intuitive classifications. In fact, because *Digitaria* has been aligned with various genera from various subtribes, the utility of the existing subtribal classifications and relationships within those subtribes are questionable. Other analytical approaches will be required to shed light on the relationships between *Digitaria* and other panicoids.

Digitaria has been relatively well studied cytologically. Polyploidy is prevalent in several species complexes, including the *D. sanguinalis* and *D. eriantha* groups. Pollen size differences were found to correlate with ploidy differences between the closely related *D. sanguinalis* (tetraploid) and *D. adscendens* (= *D. ciliaris*; hexaploid) (Gould, 1963).

Apomixis has been documented in the genus. *Digitaria valida*, a member of the *D. eriantha* complex, produces both normal and apomictic embryo sacs in the same inflorescence, with 50–60 percent of ovules developing apomictic embryo sacs. Nothing is known about the control of apomictic development in this system, but it does not always appear to be strongly correlated with meiotic irregularities. Plants of *D. valida* with normal chromosome complements of $2n = 18$ or 36 showed regular bivalent formation, and aneuploid forms with $2n = 24$, 30 , 38 , and 42 exhibited bivalent formation or occasionally a few (1–4) univalents (Purcell; Virkki & Purcell). Other workers have noted abnormal micro- and megagametogenesis in connection with substantial meiotic irregularities in the same species (a form with $2n = 42$), but no examination of apomictic reproduction was conducted (Sotomayor-Ríos *et al.*).

Davide (1987) has briefly considered dispersal mechanisms in *Digitaria*. He thought it likely that the propagules of most species of *Digitaria* are dispersed through adhesion, presumably a result of the pubescence on the glumes and proximal lemma. However, an examination of some weedy species (e.g., *D. sanguinalis*) suggests that most

fruits are shed in the vicinity of the parent plant. The distal lemma readily detaches from the rachilla. At least in the case of *D. cognata*, dispersal of the entire inflorescence occurs through the agency of wind, in the form of a 'tumbleweed' (Davidse, 1987). He also suggested that prominently hairy spikelets might be dispersed by wind as well as by adhesion, but relevant observations are not available for *Digitaria*.

The economic importance of several species of *Digitaria* is well known. Some (e.g., *D. sanguinalis*, *D. Ischaemum*) are serious weeds of lawns and cultivated ground throughout the world. Webster (1980) has noted that *D. bicornis* is becoming an important invader of cultivated soils on the Coastal Plain in our area, and is also invading natural habitats such as pine woods and oak savannahs in eastern Texas. Several of these species are also sporadic to frequent adventives emerging from bird food sources (Hanson & Mason). *Digitaria longiflora* (Retz.) Pers., India crabgrass, which is adventive in the Southeast, and *D. californica* (Bentham) Henr., Arizona cottontop, serve as hosts for two strains of maize dwarf mosaic virus and for sugarcane mosaic virus (Rosenkranz).

Other species are major wild and/or cultivated forage plants. *Digitaria californica* has been characterized as highly palatable to livestock, and it is tolerant of relatively heavy grazing, with shoots at all developmental stages present during most of the growing season because of weak apical dominance and resultant axillary shoot development (Cable). It is a dominant species in semidesert grassland vegetation. The giant pangola grass, *D. valida*, is also palatable to cattle and has a relatively high yield. It has been cultivated in Puerto Rico and Florida (Brenes *et al.*; Hall). *Digitaria insularis* has been used as a diuretic and also decoratively in the weaving of hats. It is apparently not readily grazed, however (Morton).

REFERENCES:

Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; BRENES *et al.*; CHASE (1906); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1975); HALL; HANSON & MASON; HITCHCOCK & CHASE (1951); HUGHES; JONES & COILE; MACROBERTS; MORTON; NASH (1903); OHWI; PLATZER; POHL (1976, 1980); RADFORD *et al.*; ROSENKRANZ; SHINNERS (1944); E. SMITH; STAPF (1917-1930); TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.

BOR, N. L. The genus *Digitaria* Heist. in India and Burma. *Webbia* 11: 301-367. 1955.

CABLE, D. R. Ecology of Arizona cottontop. U.S. Dep. Agr. Forest Serv. Res. Pap. RM-209. 21 pp. 1979. [Ecology and agronomic features of *Trichachne* (= *Digitaria*) *californica*.]

CHEVALIER, A. Sur l'origine des *Digitarias* cultivées. *Revue Int. Bot. Appl. Agr. Trop.* 30: 329, 330. 1950. [*D. exilis* Stapf and *D. iburua* Stapf known only in cultivation; the former may have arisen from *D. longiflora*, and the latter is most similar to *D. ternata*.]

CHRISTOPHER, J. In: IOPB chromosome number reports. LII. *Taxon* 25: 341-346. 1976. [*D. setigera*, *n* = 27.]

- CLAYTON, W. D. Notes on the genus *Digitaria* Haller. Kew Bull. **29**: 517-525. 1974a. [*Digitariella* DeWinter and *Digitariopsis* C. E. Hubbard submerged in *Digitaria*; convergent development of spurred distal glumes in different parts of the genus.]
- . A discriminant function for *Digitaria diagonalis*. Kew Bull. **29**: 527-533. 1974b. [Variation in *D. diagonalis* examined using multiple discriminant functions; three varieties recognized.]
- DE AGRASAR, Z. E. R. Las especies del género *Digitaria* (Gramineae) de la Argentina. Darwiniana **19**: 65-166. 1974. [Excellent illustrations; 29 taxa treated in five sections; one new section described.]
- EBINGER, J. E. Validity of the grass species *Digitaria adscendens*. Brittonia **14**: 248-253. 1962. [Distinctions between *D. adscendens* (= *D. ciliaris*) and *D. sanguinalis*.]
- . *Digitaria sanguinalis* in South America. Trans. Illinois Acad. Sci. **58**: 255-258. 1965. [Distributional areas of *D. sanguinalis* and *D. adscendens* (= *D. ciliaris*) strongly correlated with average winter temperature.]
- . A new form of *Digitaria sanguinalis*. Rhodora **76**: 57-58. 1974. [Forma *illinoensis*.]
- EDWARDS, G. E., & C. C. BLACK. Isolation of mesophyll cells and bundle sheath cells from *Digitaria sanguinalis* (L.) Scop. leaves and a scanning microscopy study of the internal leaf cell morphology. Pl. Physiol. **47**: 149-156. 1971.
- EMERY, W. H. P., & W. V. BROWN. Extra-ovular development of embryos in two grass species. Bull. Torrey Bot. Club **84**: 361-365. 1957. [Apomictic embryo development in *D. valida*.]
- FARWELL, O. A. "*Digitaria*" versus "*Syntherisma*". Am. Midl. Nat. **12**: 138, 139. 1930. [*Digitaria* is acceptable as presently used, with *Panicum sanguinale* L. as type.]
- GATES, F. E. Variegated plants of crabgrass. Am. Bot. **38**: 25-26. 1932. [Leaf blotching and striping described.]
- GOETGHEBEUR, P., & P. VAN DER VEKEN. Studies in Poaceae. 2. A new species of *Digitaria* section *Calvulae*, and a reexamination of *Digitariopsis* and *Digitaria* sections *Flaccidulae* and *Monodactylae*. Landbouwhogeschool Wageningen Misc. Pap. **19**: 145-153. 1980. [*Digitariopsis* lumped with *Digitaria*.]
- GOULD, F. W. Cytotaxonomy of *Digitaria sanguinalis* and *D. adscendens*. Brittonia **15**: 241-244. 1963. [Pollen size corresponds to ploidy level; *D. sanguinalis* is tetraploid; *D. adscendens* is hexaploid.]
- HENRARD, J. T. Monograph of the genus *Digitaria*. xxi + 999 pp. Leiden. 1950. [Worldwide monograph; many illustrations; species and sectional concepts liberal.]
- HITCHCOCK, A. S. The validity of the grass genus *Digitaria*. Rhodora **29**: 114-116. 1927. [Recommends conservation of *Digitaria* as used by many early authors, with *Panicum sanguinale* L. as type.]
- HOWELL, J. T. Crabgrasses (*Digitaria*) in California. Wasmann Jour. Biol. **29**: 101, 102. 1971. [Two species occur in the state (*D. sanguinalis* and *D. Ischaemum*); reports of *D. ciliaris* are incorrect.]
- KOK, P. D. F. Notes on *Digitaria* in South Africa. Bothalia **13**: 457. 1981. [Many of STENT'S and HENRARD'S taxa in sect. *Erianthae* synonymized.]
- . Studies on *Digitaria* (Poaceae). I. Enumeration of species and synonymy. S. Afr. Jour. Bot. **3**: 184, 185. 1984. [Thirty-four spp.]
- MACKENZIE, K. K. The grass genus *Digitaria*. Rhodora **30**: 49-52. 1928. [Discussion of the earliest use of *Digitaria*, noting that it is a synonym of *Paspalum* in that sense.]
- MAYNE, B. C., G. E. EDWARDS, & C. C. BLACK. Spectral, physical, and electron transport activities in the photosynthetic apparatus of mesophyll cells and bundle-sheath cells of *Digitaria sanguinalis* (L.) Scop. Pl. Physiol. **47**: 600-605. 1971. [Complete electron transport system in both cell types, but

bundle sheath cells have three times the activity of photosystem I relative to photosystem II as mesophyll cells do.]

- NASH, G. V. The genus *Syntherisma* in North America. Bull. Torrey Bot. Club 25: 289-303. 1898. [An early monograph of *Digitaria* in North America; new species and combinations.]
- PORTÈRES, R. Les céréales mineures du genre *Digitaria* en Afrique et en Europe. V. Catalogue des appellations génériques et variétales de *Digitaria exilis*. Jour. Agr. Trop. Bot. Appl. 2: 620-675. 1955. [Nomenclature of common and native names, with notes on agronomic properties, uses, distribution, yield, diseases; also a detailed bibliography.]
- PURCELL, C. M. Embryo-sac development in two accessions of giant pangola *Digitaria valida* Stent. Jour. Agr. Univ. Puerto Rico 49: 477-483. 1965. [Apomixis.]
- REEDER, J. R. In: IOPB chromosome number reports. XI. Taxon 16: 215-222. 1967. [*D. horizontalis*, $2n = 36$.]
- RUMPHO, M. E., M. E. WESSINGER, & G. E. EDWARDS. Influence of organic phosphates on 3-phosphoglycerate dependent O_2 evolution in C_3 and C_4 mesophyll chloroplasts. Pl. Cell Physiol. 28: 805-813. 1987. [*D. sanguinalis* (C_4) compared with *Hordeum vulgare* L. (C_3).]
- SHAMBULINGAPPA, K. G. Occurrence and meiotic behaviour of B chromosomes in *Digitaria*. Cytologia 33: 539-544. 1968. [B chromosomes (in *D. decumbens*, *D. Pentzii*, and *D. valida*) hypothesized to have arisen from the fragmentation of heterochromatin from regular chromosomes.]
- . Cytomorphological and sterility studies in *Digitaria Polevansii* Stent. Jour. Agr. Univ. Puerto Rico 53: 106-112. 1969.
- . Cytological studies in *Digitaria Pentzii* Stent. Ibid. 54: 401-408. 1970.
- SHIMIZU, M. On the relation between the reaction of soil and the germination and growth of *Digitaria ciliaris* Pers. (In Japanese; English summary.) Bot. Mag. Tokyo 62: 39-42. 1949. [*D. ciliaris* germinates best on acidic soils and grows best on slightly acidic to circumneutral soils.]
- SHINNERS, L. H. *Digitaria Ischaemum* (Gramineae) in Mississippi and Texas. Sida 1: 380, 381. 1964. [Spreading southward.]
- SOTOMAYOR-RÍOS, A., K. F. SCHERTZ, R. WOODBURY, & J. V. FORTUÑO. Taxonomic description and reproductive behavior of giant pangola (*Digitaria valida* Stent). Jour. Agr. Univ. Puerto Rico 44: 53-59. 1960. [Extremely low fertility; irregular meiosis.]
- SRIVASTAVA, A. K. Study of leaf epidermis in the genus *Digitaria* Rich. (Gramineae). Jour. Indian Bot. Soc. 57: 155-160. 1978.
- STENT, S. M. South African Gramineae. Some new species of *Digitaria*. Bothalia 3: 147-156. 1930. [Although the species of the *D. eriantha* complex are very similar, they can be distinguished by suites of correlated inflorescence characters.]
- SWALLEN, J. R. A new species of *Leptoloma* from Texas. Contr. Texas Res. Found. Bot. 1: 1. 1950. [*L. arenicola* Swallen (= *D. cognata* var. *arenicola* (Swallen) R. Webster).]
- . New species of *Digitaria* and *Trichachne*. Rhodora 65: 355-357. 1963. [West Indian species.]
- TIBA, S. D., C. T. JOHNSON, & C. F. CRESSWELL. Leaf ontogeny in *Digitaria eriantha*. Ann. Bot. II. 61: 541-549. 1988.
- TROUIN, M. Nombres chromosomiques de quelques graminées du Soudan. Adansonia II. 12: 619-624. 1972. [*D. ciliaris*, $2n = 36$.]
- VELDKAMP, J. F. A revision of *Digitaria* Haller (Gramineae) in Malesia. Notes on Malesian grasses. VI. Blumea 21: 1-80. 1973. [Many of HENRARD'S sections submerged, especially within sect. *Digitaria*; various other nomenclatural changes; revision of Malesian species.]

- VIRKKI, N., & C. M. PURCELL. Observations on the behavior, genetics, and cytology of two South African *Digitaria valida* Stent accessions in Puerto Rico. Jour. Agr. Univ. Puerto Rico 51: 269-285. 1967.
- WEBSTER, R. D. Distribution records for *Digitaria bicornis* in eastern United States. Sida 8: 352, 353. 1980.
- . A revision of the genus *Digitaria* Haller (Paniceae: Poaceae) in Australia. Brunonia 6: 131-216. 1983. [Thirty-eight spp., four newly described; standard key, as well as one based on vegetative characters.]
- . Taxonomy of *Digitaria* section *Digitaria* in North America (Poaceae: Paniceae). Sida 12: 209-222. 1987. [Phenetic analysis of North American taxa; six species recognized.]
- & S. L. HATCH. Taxonomic relationships of Texas specimens of *Digitaria ciliaris* and *Digitaria bicornis* (Poaceae). Sida 9: 34-42. 1981.
- & ———. Two *Digitaria* species (Poaceae) new to the New World. Sida 9: 87, 88. 1981. [*D. nuda*, *D. setigera*.]
- & R. B. SHAW. Relationship between *Digitaria milanjiana* (Poaceae: Paniceae) and the annual species of *Digitaria* section *Digitaria* in North America. Sida 9: 333-343. 1982. [Sect. *Erianthae* and sect. *Digitaria* distinct.]
- WIPFF, J. K., & S. L. HATCH. Nomenclatural changes in *Taeniatherum* and *Digitaria* (Poaceae). Sida 13: 119-121. 1988. [*D. cognata* subsp. *pubiflora* (Vasey ex L. H. Dewey) Wipff.]

Subtribe CENCHRINAE (Dumortier) Dumortier, Fl. Belg. 149. 1827.

3. *Pennisetum* L. C. Richard in Persoon, Syn. Pl. 1: 72. 1805.

Rhizomatous, stoloniferous, decumbent, or caespitose perennials or annuals. Stems 15-400 [800] cm high, branched or unbranched above; internodes spongy to hollow, occasionally glaucous; nodes glabrous or pubescent. Leaves cauline [mostly basal], with sheaths glabrous or pubescent; ligule a fringed membrane or a fringe of hairs [membrane]; blades linear to lanceolate, flat or folded, glabrous, scabrous or pubescent, cuneate to truncate at base, disarticulating from the sheath or not, rolled or once-folded in bud; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences paniculate, contracted and spike-like, with fascicles of spikelets on reduced axes that disarticulate; rachis terminating in a bristle; bristles subtending spikelets free, [1] 20-100, slender, often plumose, disarticulating with spikelets. Spikelets lanceolate to obovate, dorsiventrally compressed, disarticulating below the glumes or reduced axes disarticulating with spikelets attached, abaxial, secund or not, sessile or pedicellate (pedicel apices cupuliform), solitary or in fascicles of 2-6; proximal florets staminate or sterile, paleate or epaleate. Calli undifferentiated or prolonged, hairy. Glumes 1 or 2, unequal, membranaceous, glabrous or pubescent, acuminate to truncate, awnless; proximal glumes 0 [-5] nerved; distal glumes longer to shorter than proximal lemmas, ovate, 0-5 [-11] nerved. Proximal lemmas shorter than [equalling], and similar in texture or less firm than distal lemmas, glabrous, acuminate to obtuse, awnless, 3-5 [-15] nerved; distal lemmas chartaceous to cartilaginous, smooth or scabrous, glabrous or pubescent, acuminate to obtuse, awnless or mucronate, [3-] 5-7 nerved,

with flat or involute margins and with or without a conspicuous germination flap. Distal paleas similar in texture to distal lemma, acute, awnless, 2 keeled. Lodicules 0 or 2. Ovaries with styles fused or free, stigmas white or red. Caryopses (grains) small, smooth; endosperm hard, without lipid, containing only simple starch grains. (Including *Beckeropsis* Figari & De Not., *Eriochaeta* Figari & De Not.) Base chromosome number probably 9. LECTOTYPE SPECIES: *Pennisetum americanum* (L.) Leeke (*P. typhoideum* L. C. Rich.); see Hitchcock, U.S. Dep. Agr. Bull. 772: 245. 1920. (Name from Latin, *penna*, feather, and *seta*, bristle.) — MILLET, NAPIERGRASS, ELEPHANTGRASS, FOUNTAINGRASS, PENNISETUM, FEATHERTOP.

A genus mainly of tropical latitudes, consisting of about 100 species and occurring in natural grasslands, savannahs, woodlands, and cultivated fields, orchards, and waste areas. There is no satisfactory modern treatment of the genus, although parts of it have been revised. Some authors separate *Beckeropsis* Figari & De Not. on the basis of the single bristle subtending each spikelet and the inflorescence consisting of several branches arising from the upper nodes of the stem rather than being strictly terminal (Chippindall). However, morphological intermediates exist (Bentham; Clayton & Renvoize; Roshevits). Roshevits delineated six sections (sect. *Gymnotrix* (Beauv.) Spreng.; sect. *Pennisetum*; sect. *Penicillaria* (Willd.) Steudel; sect. *Beckeropsis* (Figari & De Not.) Hackel; sect. *Heterostachya* Stapf; and sect. *Brevivalvula* Stapf). Brunken (1977) included sect. *Penicillaria* in sect. *Pennisetum*. Two-thirds of the species are in sect. *Gymnotrix* (Clayton & Renvoize; Leeke). Africa is the center of diversity of the genus (Chase, 1921).

Four species in two sections have been recorded as escapes from cultivation and are naturalized in our area. The two species in sect. PENNISETUM (anther tips penicillate, bracts of distal floret indurate, bristles plumose, $x = 7$) are *P. purpureum* Schum., napiergrass, elephantgrass, $n = 14$ (perennial, internodes glaucous) and *P. americanum* (L.) Leeke (*P. glaucum* auct., non (L.) R. Br., *P. typhoideum* L. C. Rich., *P. typhoides* (Burm. f.) Stapf & C. E. Hubb.), pearl millet, shibra, babala, $n = 7$ (annual, internodes glabrous). *Pennisetum purpureum* is a weed. *Pennisetum americanum* is extremely variable. Three subspecies based on morphology and ecological/agronomic behavior are presently recognized within it (Brunken, 1977; Brunken *et al.*). The cultivated pearl millet (*P. americanum* subsp. *americanum*) has been grown in the Southeast, but it does not persist without cultivation, and has lost the ability to disperse effectively. It has been selected for non-shattering inflorescences. The mimetic weed, shibra, *P. americanum* subsp. *stenostachyum* (Klotsch) Brunken, can persist without cultivation and develops a sharp, well-defined callus that assists in dispersal. There is no evidence that the wild form, *P. americanum* subsp. *Monodii* (Maire) Brunken, native to the West African sahel, has become naturalized in the Southeast. The other two naturalized species

are members of sect. *BREVIVALVULA* (anther tips glabrous, glumes and proximal lemma membranaceous, bracts of distal floret indurate, bristles plumose or merely scabrous, apex of proximal lemma tridentate, rachis below each involucre with decurrent wings, $x = 9$). *Pennisetum pedicellatum* Trin. subsp. *pedicellatum*, $2n = 36, 45, 52, 54$ (involucre subtending one or more pedicellate spikelets, bristles scabrous) and *P. polystachion* (L.) Schultes subsp. *setosum* (Sw.) Brunken (*P. setosum* (Sw.) L. C. Rich.), $2n = 54, 56$ (involucre subtending single sessile spikelets, bristles plumose) are apomictic weeds (Brunken, 1979a, b).

Many other species have been cultivated for experimental purposes or as ornamentals, but they have not yet become naturalized in the Southeast (Gould, 1975; Hall). *Pennisetum* (*Beckeropsis*) *petiolare* (Hochst.) Chiov., has been found as an adventive arising from commercial bird seed in Iowa (Pohl, 1987).

Pennisetum and *Cenchrus* are very closely related. Several species that are now generally included in *Cenchrus* had previously been assigned to *Pennisetum* (e.g., *C. ciliaris* L.; Chase, 1921; Pohl, 1980; Richard; Sohns, 1955). There is no doubt that *C. ciliaris* and a few other Old World species of *Cenchrus* approach *Pennisetum* morphologically, but the involucre bristles in *Cenchrus* always exhibit some degree of fusion, at least basally, and this is never the case in *Pennisetum* (Webster, 1988). A cladistic analysis of subtribe Cenchrinae may establish the arbitrariness of this distinction, however.

The close relationship between *Pennisetum* and *Cenchrus* is evident in the phenetic analysis of Watson & Dallwitz. Other genera in their analysis that exhibit close phenetic similarities with *Pennisetum*, or with its segregate *Beckeropsis*, include *Stenotaphrum* Trin., *Strepitophus* Hughes, *Panicum* L., *Chlorocalymma* Clayton, *Digitaria*, and *Paspalidium* Stapf. However, these genera are spread among three subtribes in the classification adopted here. Clayton & Renvoize consider *Pseudochaetochloa* Hitchc. to be another close relative of *Pennisetum*.

The only modern attempt to assess relationships within *Pennisetum*, and between *Pennisetum* and *Cenchrus*, utilized chloroplast DNA restriction endonuclease site polymorphisms. Clegg *et al.* found differences in both interspecific and intergeneric comparisons of restriction sites in the small and large single-copy regions of the chloroplast DNA genomes. This is a tantalizing bit of preliminary information on the utility of the method, but many more species from both genera must be examined before relationships can be resolved more fully.

Pennisetum contains several economically important species. For this reason, considerable effort has been expended in determining the nature of variation in pearl millet (*P. americanum*) and its relatives. Since pearl millet is a variable diploid, out-crossing species (Brunken *et al.*), many agronomists have attempted to stabilize desirable variation by hybridization with apomictic species. The aim has been to develop uniform clones that would be disease-resistant and have high yields

and stable morphology (Hanna & Monson). Inbred lines of *P. americanum* occasionally generate spontaneous autotetraploids and haploids (Hanna *et al.*; Jauhar, 1970b; Manga & Pantulu; Pantulu & Manga, 1969; Powell & Burton; Powell *et al.*), but these are generally unstable. One of the most common synthetic hybrids is that between *P. americanum* and its closest relative, *P. purpureum*. These species share one genome, and *P. purpureum* has a second genome of unknown origin that is structurally differentiated from that of *P. americanum*. The triploid F₁ hybrids have highly irregular meioses, pollen stainability that ranges from 0 to 84 percent, and over 99 percent of the megaspores abort (Hanna, 1981; Raman & Krishnaswamy, 1959; Ramulu; Sethi *et al.*). Gildenhuys & Brix (1961, 1964) conducted a series of experiments with hybrids of this parentage, including the production of colchicine-induced hexaploids. These hexaploids were fertile (i.e., set seed) but were extremely unstable in somatic chromosome number ($2n = 36$ to 49). They concluded that aneuploidy was under genic control. However, this needs confirmation. Somatic chromosome number stabilized at about $2n = 21$ after one year, allegedly through chromosome elimination and elimination of highly reduced cells. Tetraploid plants of hybrid origin have arisen in some experiments, presumably through fertilization by or from an unreduced gamete of *P. americanum*. Selfed progeny from these allotetraploid hybrids are unstable in their chromosome complements ($2n = 28$ or 42; Raman & Krishnaswamy, 1961).

Other experimental crosses have involved *Pennisetum americanum* with *P. orientale* L. C. Rich. (Dujardin & Hanna, 1983a; Hanna & Dujardin; Patil & Singh), *P. setaceum* (Forsskål) Chiov. (*P. Ruppellii* Steudel) (Hanna, 1979), and *P. squamulatum* Fresen. (Dujardin & Hanna, 1985, 1987). Apomixis has been documented in several species. *Pennisetum divisum* (Forsskål) Henr. and *P. setaceum* are both facultative apomicts, and at least in the latter, pseudogamy is necessary for seed set (Simpson & Bashaw). The frequency of multiple embryo sacs is much greater in *P. divisum*, but polyembryony was observed only in *P. setaceum* (Inamuddin & Faruqi). All of the taxa in sect. *Brevivalvula* are agamospermous (at least facultatively) (Brunken, 1979a). *Pennisetum squamulatum*, *P. orientale*, and *P. flaccidum* Griseb. are also apomictic (Chatterji & Timothy, 1969a, b; Dujardin & Hanna, 1983b; Hanna & Dujardin).

Polyploidy is common in *Pennisetum*, as it is in most genera of the tribe. Aneuploidy has also occurred several times. The existence of several basic chromosome numbers attests to this ($x = 5, 7, 8, 9, 17$; Rangasamy; Swaminathan & Nath). The base number 17 must be a derivative of a tetraploid with $n = 18$, although the suggestion was not made by Shanthamma, who studied a plant of *P. macrostachyum* Benth. (= *P. purpureum*; see Bor, 1960) with this base number. It seems likely that $x = 9$ is the base number of the genus because many other genera of the tribe have this base number, and it is probably the number from which the base number of its closest relative, *Cenchrus* ($x = 17$), is derived. However, an argument in favor of $x = 5$ as the basic

number of *Pennisetum* has been put forth by Swaminathan & Nath (supported by Jauhar, 1970a, b) on the basis of the meiotic behavior of a monosomic autotetraploid that survived to maturity. Various other aneuploids have been reported (Jauhar 1970a; Pantulu & Manga, 1972; Rao *et al.*; Vari & Bhowal), as have plants with B chromosomes (Arundhati & Pantulu; Pantulu; Venkateswarlu & Pantulu).

Some attempts have been made to grow embryos of hybrids by the use of tissue culture (Narayanawami, 1959; Vasil & Vasil, 1981a, b, 1982).

Limited data are available on the genetic variability within species of *Pennisetum*. Three alcohol dehydrogenase isozymes exist in *P. americanum*, and these are coded by two structural genes (Banuett-Bourrillon, 1982a, b; Banuett-Bourrillon & Hague). Variability also exists in the response of pearl millet lines to salt stress, but the genetic basis for this variability is not yet known (Bouraima *et al.*). Pollen tube competitive ability among pearl millet lineages also has a genetic basis and is thought to be polygenic (Sarr *et al.*).

Pollination is generally mediated by wind, but insects may also play a minor role in cross-pollination (Leuck & Burton). The nature of the incompatibility system in *Pennisetum* is still poorly understood, although stigmatic secretions and constriction may contribute to pollen tube selection (Connor, 1987; Reger; Willingale & Mantle).

Pennisetum americanum has been used as an experimental organism for the determination of the effects of environmental factors and plant hormones on metabolic enzyme activities. Absciscic acid inhibited the activities of amylase, invertase, and glutamate dehydrogenase, and stimulated the activities of phosphorylase, hexose-phosphate-isomerase, sucrose-6-phosphate-synthetase, sucrose-synthetase, and alanine and aspartate aminotransferases. Gibberellic acid (GA3) promoted the activity of invertase but on its own had no significant effect on the activities of the other enzymes. However, in combination with absciscic acid, it tended to antagonize the effects of the latter (Huber & Sankhla; Sankhla & Huber). Variability in the activities of phosphoenolpyruvate carboxylase and NADP-malic enzyme in four genotypes of pearl millet in response to mild sodium chloride stress may also serve as a marker for salt tolerance (Bouraima *et al.*). Salt had much the same effect as absciscic acid in the genotype used by Huber & Sankhla, and its effect was again counteracted by gibberellic acid.

The fruits of most species of *Pennisetum* are dispersed by wind. The modified bristles subtending the fascicles of spikelets clearly facilitate anemophily. However, one species, *Pennisetum clandestinum*, Kikuyu grass, has cleistogamous spikelets that remain enclosed within the leaf sheaths. Dispersal of the propagules in this species is accomplished when ungulates ingest the vegetative material. Fruits are dispersed when they pass through the digestive tract unscathed (Janzen).

Pearl millet is the sixth most important cereal crop in the world and is one of the most drought-tolerant grains (Brunken *et al.*; Jauhar, 1981). Its digestibility does not decrease upon cooking, and it is considered

to be a nutritious source of calories and proteins for humans (Ejeta *et al.*). It is attacked by a scrophulariaceous parasite, *Striga hermonthica* (Del.) Benth. in Africa (Ba), but the effect of this interaction on yield is undocumented.

Several species have been cultivated as pasture grasses (*Pennisetum purpureum*, *P. clandestinum*, *P. flaccidum*) or as ornamentals for their large, often purplish inflorescences. *Pennisetum clandestinum* has also been used for soil stabilization (Webster, 1988). *Pennisetum purpureum* is known to be highly palatable to livestock (Arroyo & Brenes; Brenes *et al.*). *Pennisetum polystachion* subsp. *setosum* has been used in Central America in the treatment of seasickness (Morton).

A few species are troublesome weeds in tropical areas, for example, *Pennisetum polystachion* subsp. *setosum* in the New World (Brunken, 1979). *Pennisetum clandestinum*, although highly palatable to livestock and grown as a forage grass, is also capable of outcompeting many native grassland species, and it has become a weed in several areas (Matthei & Rodríguez; Stapf, 1921; Webster, 1988). *Pennisetum macrourum* Trin., African feather grass, is a problematic weed in Tasmania, where it is difficult to control because of its capability for vegetative regeneration (Harradine, 1980a, b). At least two species of *Pennisetum* may serve as alternate hosts for maize dwarf mosaic virus and sugarcane mosaic virus (Rosenkranz).

REFERENCES:

- Under references for tribe see BENTHAM; BOLKHOVSKIKH *et al.*; BOR (1960); BRENES *et al.*; CHIPPINDALL; CLAYTON & RENVOIZE; GOULD (1975); HALL; MAC-ROBERTS; MORTON; POHL (1976, 1980); RADFORD *et al.*; ROSENKRANZ; ROSHEVITS; SOHNS (1955); TSVELEV (1976); WATSON & DALLWITZ; and WEBSTER (1987, 1988).
- AL-FAKHRY, A. K., P. SARVELLA, & C. O. GROGAN. Somatic chromosomes of babala. *Jour. Hered.* **55**: 57-60. 1964. [*P. typhoides* (= *P. americanum*), $2n = 14$; karyotype drawn.]
- ARUNDHATI, A., & J. V. PANTULU. Short arm telocentric B chromosome in *Pennisetum typhoides* (Gramineae). *Cytologia* **51**: 701-705. 1986. [Transmission frequency of B chromosome 8-10 percent.]
- BA, A. T. Structure et ultrastructure de l'haustorium du *Striga hermonthica*, une scrophulariacée parasite du mil (*Pennisetum typhoides*). *Canad. Jour. Bot.* **66**: 2111-2117. 1988. [Attached to the roots of pearl millet; the *Striga* has no phloem.]
- BANUETT-BOURRILLON, F. Linkage of the alcohol dehydrogenase structural genes in pearl millet (*Pennisetum typhoides*). *Biochem. Genet.* **20**: 359-367. 1982a.
- . Natural variants of pearl millet (*Pennisetum typhoides*) with altered levels of set II alcohol dehydrogenase activity. *Ibid.* **20**: 369-383. 1982b.
- & D. R. HAGUE. Genetic analysis of alcohol dehydrogenase isozymes in pearl millet (*Pennisetum typhoides*). *Ibid.* **17**: 537-552. 1979.
- BORGEN, L. Chromosome numbers of vascular plants from the Canary Islands, with special reference to the occurrence of polyploidy. *Nytt Mag. Bot.* **16**: 81-121. 1969. [*P. elatum* Hochst. ex Steud., $2n = 27$.]
- BOURAIMA, S., J. VIDAL, D. LAVERGNE, A. HOARAU, & M.-L. CHAMPIGNY. Effects of sodium chloride stress on phosphoenolpyruvate carboxylase, NADP-malic enzyme and ribulose-1,5-bisphosphate carboxylase in shoots of pearl millet. *Phytochemistry* **26**: 1329-1332. 1987.

- BRUNKEN, J. N. A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae). *Am. Jour. Bot.* **64**: 161-176. 1977. [Biological species concept applied; two species (*P. americanum* and *P. purpureum*) recognized; intersectional and intergeneric hybrids with pearl millet are sterile.]
- . Cytotaxonomy and evolution in *Pennisetum* section *Brevivalvula* (Gramineae) in tropical Africa. *Bot. Jour. Linn. Soc.* **79**: 37-49. 1979a. [Three species, six taxa recognized; all are weedy polyploids.]
- . Morphometric variation and the classification of *Pennisetum* section *Brevivalvula* (Gramineae) in tropical Africa. *Ibid.* 51-64. 1979b. [Three phenetically distinct groups determined by principal components analysis treated as species; extremes of a continuum in morphological variation within these species treated as subspecies.]
- , J. M. J. DE WET, & J. R. HARLAN. The morphology and domestication of pearl millet. *Econ. Bot.* **31**: 163-174. 1977. [Three subspecies recognized within *P. americanum*; biological species concept applied.]
- BURTON, G. W. Factors affecting pollen movement and natural crossing in pearl millet. *Crop Sci. Madison* **14**: 802-805. 1974.
- CHAFFEY, N. J. Structure and function in the grass ligule: presence of veined and membranous ligules on the same culm of British grasses. *New Phytol.* **101**: 613-621. 1985. [Membranaceous ligules in *P. typhoides* (= *P. americanum*).]
- CHANDA, S. V., A. K. JOSHI, P. N. KRISHNAN, & Y. D. SINGH. Distribution of glycosidases and acid invertase activities in relation to elongation growth in pearl millet internode. *Jour. Exper. Bot.* **37**: 1406-1415. 1986.
- CHANDOLA, R. P., & S. N. JAIN. Karyomorphological studies in *Pennisetum typhoides* L. *Cytologia* **35**: 181-196. 1970.
- CHASE, A. The North American species of *Pennisetum*. *Contr. U.S. Natl. Herb.* **22**: 209-234. 1921. [Fourteen spp., incl. *P. ciliare* (= *Cenchrus ciliaris*).]
- CHATTERJI, A. K., & D. H. TIMOTHY. Microsporogenesis and embryogenesis in *Pennisetum flaccidum* Griseb. *Crop Sci. Madison* **9**: 219-222. 1969a.
- & ———. Apomixis and tetraploidy in *Pennisetum orientale* Rich. *Ibid.* 796-799. 1969b.
- CLEGG, M. T., J. R. Y. RAWSON, & K. THOMAS. Chloroplast DNA variation in pearl millet and related species. *Genetics* **106**: 449-461. 1984. [Reverse repeat region containing ribosomal RNA genes highly conserved relative to large and small single-copy regions, in which interspecific and intergeneric differences occur.]
- DANIEL, P., & J. J. SHAH. Some aspects of floral histogenesis in bajra (*Pennisetum typhoides* S. & H.). *Ann. Bot. II.* **35**: 373-387. 1971.
- DUJARDIN, M., & W. W. HANNA. Meiotic and reproductive behavior of facultative apomictic BC1 offspring derived from *Pennisetum americanum*-*P. orientale* interspecific hybrids. *Crop Sci. Madison* **23**: 156-160. 1983a.
- & ———. Apomictic and sexual pearl millet × *Pennisetum squamulatum* hybrids. *Jour. Hered.* **74**: 277-279. 1983b.
- & ———. Cytology and reproduction of reciprocal backcrosses between pearl millet and sexual and apomictic hybrids of pearl millet × *Pennisetum squamulatum*. *Crop Sci. Madison* **25**: 59-62. 1985.
- & ———. Cytotaxonomy and evolutionary significance of two offtype millet plants derived from a pearl millet × (pearl millet × *Pennisetum squamulatum*) apomictic hybrid. *Jour. Hered.* **78**: 21-23. 1987.
- EJETA, G., M. M. HASSEN, & E. T. MERTZ. In vitro digestibility and amino acid composition of pearl millet (*Pennisetum typhoides*) and other cereals. *Proc. Natl. Acad. Sci. U.S.A.* **84**: 6016-6019. 1987. [Pearl millet more digestible than sorghum and comparable to maize.]
- GADELLA, T. W. J., & E. KLIPHUIS. Chromosome numbers of some flowering plants collected in Surinam. *Acta Bot. Neerl.* **13**: 432, 433. 1964. [*P. purpureum* cultivar Uganda, 2n = 56.]

- GILDENHUYS, P., & K. BRIX. Cytological abnormalities in *Pennisetum dubium*. Heredity **12**: 441-452. 1958. [*P. dubium* nom. inval.; probably = *P. macrourum* Trin.; chromosome number highly variable.]
- & ———. Genic control of aneuploidy in *Pennisetum*. *Ibid.* **16**: 358-363. 1961. [Hybrid of *P. typhoides* (= *P. americanum*) and *P. purpureum* had variable chromosome numbers in root tips for the first year, but chromosome number stabilized at or near $2n = 21$; irregular chromosome behavior in hybrid of *P. typhoides* and *P. dubium*.]
- & ———. Genically controlled variability of chromosome number in *Pennisetum* hybrids. *Ibid.* **19**: 533-542. 1964. [Dubious interpretations.]
- HANNA, W. W. Interspecific hybrids between pearl millet and fountaingrass. Jour. Hered. **70**: 425-427. 1979. [*P. americanum* and *P. orientale*.]
- . Method of reproduction in napiergrass and in the $3x$ and $6x$ allopolyploid hybrids with pearl millet. Crop Sci. Madison **21**: 123-126. 1981. [*P. americanum* and *P. purpureum*.]
- & M. DUJARDIN. Apomictic interspecific hybrids between pearl millet and *Pennisetum orientale* L.C. Rich. Crop Sci. Madison **22**: 857-859. 1982.
- & W. G. MONSON. Yield, quality, and breeding behavior of pearl millet \times napiergrass interspecific hybrids. Agron. Jour. **72**: 358-360. 1980. [Variability in *P. purpureum* clones.]
- , J. B. POWELL, & G. W. BURTON. Relationship to polyembryony, frequency, morphology, reproductive behavior, and cytology of autotetraploids in *Pennisetum americanum*. Canad. Jour. Genet. Cytol. **18**: 529-536. 1976. [Polyembryony and tetraploidy highly correlated.]
- HARRADINE, A. R. The biology of African feather grass (*Pennisetum macrourum* Trin.) in Tasmania, I. Seedling establishment. Weed Res. **20**: 165-169. 1980a; II. Rhizome biology. *Ibid.* 171-175. 1980b.
- HEDBERG, O. Afroalpine vascular plants. A taxonomic revision. Symb. Bot. Upsal. **15**: 1-411. 1957. [*P. clandestinum*, $2n = 36$.]
- HUBER, W., & N. SANKHLA. Eco-physiological studies on Indian arid zone plants. II. Effect of salinity and gibberellin on the activity of the enzymes of amino acid metabolism in leaves of *Pennisetum typhoides*. Oecologia **13**: 271-277. 1973. [Growth inhibition, reduced glutamate dehydrogenase activity, enhanced alanine and aspartate aminotransferase activities at high salt concentration; GA counteracts effects of salt.]
- , & H. ZIEGLER. Eco-physiological studies on Indian arid zone plants. I. Photosynthetic characteristics of *Pennisetum typhoides* (Burm. f.) Stapf & Hubbard and *Lasiurus scindicus* Henr. Oecologia **13**: 65-71. 1973. [Highly labelled malate and alanine from brief exposure to $^{14}\text{CO}_2$.]
- INAMUDDIN, M., & S. A. FARUQI. Studies in Libyan grasses. VIII. Apomixis in *Pennisetum divinum sensu lato* and *P. setaceum* (Forssk.) Chiov. Pakistan Jour. Bot. **14**: 69-74. 1982. [Both facultative apomicts.]
- JANZEN, D. H. Dispersal of small seeds by big herbivores: foliage is the fruit. Am. Nat. **123**: 338-353. 1984. [*P. clandestinum*.]
- JAUHAN, P. P. Chromosome behaviour and fertility of the raw and evolved synthetic tetraploids of pearl millet, *Pennisetum typhoides* Stapf et Hubb. Genetica **41**: 407-424. 1970a. [High frequency of multivalents present in early generations of the autotetraploid; pairing by the sixth generation was largely in the form of bivalents, and seed set improved considerably.]
- . Haploid meiosis and its bearing on the phylogeny of pearl millet, *Pennisetum typhoides* Stapf et Hubb. Genetica **41**: 532-540. 1970b. [Close associations among chromosomes at meiosis suggests the possibility that the base chromosome number for pearl millet is 5.]
- KARPER, R. E., & A. T. CHISHOLM. Chromosome numbers in *Sorghum*. Am. Jour. Bot. **23**: 369-374. 1936. [*P. glaucum* (= *P. americanum*), $n = 7$.]

- KU, S. B., M. GUTIERREZ, & G. E. EDWARDS. Localization of the C₄ and C₃ pathways of photosynthesis in the leaves of *Pennisetum purpureum* and other C₄ species. Insignificance of phenol oxidase. *Planta* **119**: 267-278. 1974.
- LEEKE, P. Untersuchungen ber Abstammung und Heimat der Negerhirse [*Pennisetum americanum* (L.) K. Schum.]. *Zeitschr. Naturw.* **79**: 1-108. 1907. [World monograph, seventy-six spp.; origin and relationships of pearl millet.]
- LEUCK, D. B., & G. W. BARTON. Pollination of pearl millet by insects. *Jour. Econ. Entomol.* **59**: 1308, 1309. 1966. [Bees (*Apis*, *Bombus*) pollinating male-sterile clones; but pollination probably largely by wind.]
- MANGA, V., & J. V. PANTULU. The meiotic behaviour of a haploid pearl millet. *Genetica* **42**: 319-328. 1971. [Apparent random pairing in the haploid; does not reflect chromosome homology, contrary to the suggestion of JAUHAR (1970).]
- MATTHEI, O., & R. RODRÍGUEZ. Dos malezas nuevas para Chile. *Gayana Bot.* **44**: 55-59. 1987. [*P. clandestinum*, a new weed in Chile, illustrated.]
- NARAYANASWAMI, S. The structure and development of the caryopsis in some Indian millets. 1. *Pennisetum typhoideum* Rich. *Phytomorphology* **3**: 98-112. 1953. [Individual bristles are reduced branches; no lodicules in this species; megasporogenesis and microsporogenesis normal.]
- . Experimental studies on growth of excised grass embryos in vitro. I. Overgrowth of the scutellum of *Pennisetum* embryos. *Phytomorphology* **9**: 358-367. 1959. [Tissue culture.]
- PANTULU, J. V. Accessory chromosomes in *Pennisetum typhoides*. *Curr. Sci. Bangalore* **29**: 28, 29. 1960. [From 0-3 B-chromosomes in root tips.]
- & V. MANGA. Meiosis in a haploid pearl millet. *Ibid.* **38**: 143, 144. 1969. [Secondary associations form among chromosomes, but highly irregular pollen grain formation and meiotic divisions.]
- & ———. Cytogenetics of 16 chromosome plants in pearl millet. *Cytologia* **37**: 389-394. 1972. [Meiotic abnormalities induced by B chromosomes.]
- PATIL, B. D., M. W. HADRAS, & A. B. JOSHI. Auto-allopolyploid nature of *Pennisetum squamulatum* Fresen. *Nature* **189**: 419, 420. 1961.
- & A. SINGH. An interspecific cross in the genus *Pennisetum* involving two basic numbers. *Curr. Sci. Bangalore* **33**: 255. 1964. [Homeology appears to exist between the chromosomes of *P. typhoides* (= *P. americanum*), *n* = 7, and *P. orientale*, *n* = 9.]
- POHL, R. W. *Pennisetum petiolare*, a pseudopetiolate African grass adventive in Iowa. *Proc. Iowa Acad. Sci.* **94**: 20, 21. 1987. [Illustrated.]
- POWELL, J. B., & G. W. BURTON. Polyembryony in pearl millet, *Pennisetum typhoides*. *Crop Sci. Madison* **8**: 771-773. 1968.
- , W. W. HANNA, & G. W. BURTON. Origin, cytology, and reproductive characteristics of haploids in pearl millet. *Ibid.* **15**: 389-392. 1975.
- RAJU, M. S., V. SESHAVATHARAM, & S. A. RAO. Contribution to the leaf anatomy of the genus *Pennisetum* Rich. *Proc. Indian Acad. Sci. Pl. Sci.* **96**: 113-120. 1986. [Key to eighteen species based on epidermal characters.]
- RAMAN, V. S., & D. KRISHNASWAMY. Studies on the interspecific hybrid of *Pennisetum typhoides* × *P. purpureum*. V. The cytology of an allotriploid plant. *Jour. Indian Bot. Soc.* **39**: 382-385. 1959.
- & ———. Studies on the interspecific hybrid of *Pennisetum typhoides* × *P. purpureum*. VI. The cross derivatives of the allotetraploid. *Ibid.* **40**: 61-65. 1961.
- RAMANA, T., & T. M. RADHAKRISHNAN. De novo synthesis of protease during germination of pearl millet seeds. *Curr. Sci. Bangalore* **56**: 397-400. 1987.
- RAMULU, K. S. Meiosis and fertility in derivatives of amphiploid *Pennisetum*. *Caryologia* **21**: 147-156. 1968.
- RANGASAMI, K. On the cytology of *Pennisetum typhoideum* Rich. *Jour. Indian Bot. Soc.* **14**: 125-131. 1935. [*n* = 7.]

- RANGASAMY, S. R. S. Cytological studies on diploid and polyploid taxa of the genus *Pennisetum* Rich. *Genetica* **43**: 257-273. 1972. [Morphologically defined sections do not correspond to cytological groups.]
- RAO, M. K., K. A. KUMARI, & J. R. GRACE. Cytology of antipodal cells with some observations on the male and female gametophyte development in pearl millet, *Pennisetum americanum* (L.) Leeke. *Bot. Gaz.* **144**: 201-206. 1983.
- RAO, P. N., P. RANGANADHAM, & A. NIRMALA. Twins and triplets in pearl millet: their cytology and origin. *Ann. Bot. II.* **58**: 627-631. 1986.
- REGER, B. J. Stigma surface secretions of *Pennisetum americanum*. *Am. Jour. Bot.* **76**: 1-5. 1989. [Stigma secretion is glycoprotein with esterase activity.]
- & J. J. SPRAGUE. Pearl millet and sorghum pollen tube growth in pearl millet gynoecea of different ages. *Crop Sci. Madison* **23**: 931-934. 1983.
- RICHARD, L. C. *Pennisetum*. P. 72 in C. H. PERSOON, *Synopsis Plantarum*. Vol. 1. Paris. 1805. [5 spp.]
- SANKHLA, N., & W. HUBER. Enzyme activities in *Pennisetum* seedlings germinated in the presence of abscisic and gibberellic acids. *Phytochemistry* **13**: 543-546. 1974. [Growth and activity of glutamate dehydrogenase inhibited, activity of alanine and aspartate aminotransferases stimulated by ABA; enzyme activities unaffected by GA.]
- SARR, A., M. SANDMEIER, & J. PERNÈS. Gametophytic competition in pearl millet, *Pennisetum typhoides* (Stapf et Hubb.). *Genome* **30**: 924-929. 1988. [Absence of a hierarchical order in pollen competitive abilities among genotypes suggests polygenic control for these features.]
- SETHI, G. S., H. R. KALIA, & B. S. GHAI. Cytogenetical studies of three interspecific hybrids between *Pennisetum typhoides* Stapf and Hubb. and *P. purpureum* Schumach. *Cytologia* **35**: 96-101. 1970. [Meiotic irregularities in hybrids.]
- SHANTHAMMA, C. Reproductive behavior of *Pennisetum macrostachyum* Benth., and a new basic chromosome number in the genus *Pennisetum*. *Bull. Torrey Bot. Club* **106**: 73-78. 1979. [Normal microsporogenesis and megasporogenesis; $x = 17$; $2n = 68$.]
- SIMMONDS, N. W. Chromosome behaviour in some tropical plants. *Heredity* **8**: 139-146. 1954. [*P. purpureum*, $2n = 28$.]
- SIMPSON, C. E., & E. C. BASHAW. Cytology and reproductive characteristics in *Pennisetum setaceum*. *Am. Jour. Bot.* **56**: 31-36. 1969. [Aposporous triploid and hexaploid races.]
- SISODIA, K. P. S. Cytomorphological studies in *Pennisetum orientale* Rich. *Cytologia* **37**: 309-316. 1972. [Tetraploid race is autotetraploid.]
- STAPP, O. Kikuyu grass (*Pennisetum clandestinum*, Chiov.). *Bull. Misc. Inf. Kew* **1921**: 85-93. 1921. [Illustration; agronomic properties.]
- SWAMINATHAN, M. S., & J. NATH. Two new basic chromosome numbers in the genus *Pennisetum*. *Nature* **178**: 1241, 1242. 1956. [Suggestion that $x = 5$ is the basic number; $x = 5, 8$.]
- THULIN, M. Chromosome numbers of some vascular plants from East Africa. *Bot. Not.* **123**: 488-494. 1970. [*P. Schimperi* A. Rich., $2n = 18$.]
- TÜRPE, A. M. Las especies sudamericanas del género *Pennisetum* L. C. Richard (Gramineae). *Lilloa* **36**: 105-129. 1983. [Twenty spp.; key and illustrations of spikelets.]
- VARI, A. K., & J. G. BHOWAL. Studies on the trisomics of *Pennisetum americanum* (L.) Leeke. Morphological and cytological behaviour of primary trisomics. *Cytologia* **51**: 679-692. 1986.
- VASIL, V., & I. K. VASIL. Somatic embryogenesis and plant regeneration from tissue cultures of *Pennisetum americanum*, and *P. americanum* \times *P. purpureum* hybrid. *Am. Jour. Bot.* **68**: 864-872. 1981a.
- & ———. Somatic embryogenesis and plant regeneration from suspension cultures of pearl millet (*Pennisetum americanum*). *Ann. Bot. II.* **47**: 669-678. 1981b.

- & ———. Characterization of an embryogenic cell suspension culture derived from cultured inflorescences of *Pennisetum americanum*, pearl millet (Gramineae). *Am. Jour. Bot.* **69**: 1441–1449. 1982.
- VENKATESWARLU, J., & J. V. PANTULU. The cytological behaviour of B-chromosomes in *Pennisetum typhoides*. *Cytologia* **35**: 444–448. 1970. [Variable number of B chromosomes in cells of the same root tip and in pollen mother cells of the same anther.]
- WILLINGALE, J., & P. G. MANTLE. Stigma constriction in pearl millet, a factor influencing reproduction and disease. *Ann. Bot.* **56**: 109–115. 1985.
- ZELEZNAK, K., & E. VARRIANO-MARSTON. Pearl millet (*Pennisetum americanum* (L.) Leeke) and grain sorghum (*Sorghum bicolor* (L.) Moench) ultrastructure. *Am. Jour. Bot.* **69**: 1306–1313. 1982. [Transmission and electron microscopic analysis of caryopsis.]

4. *Cenchrus* Linnaeus, *Sp. Pl.* **2**: 1409. 1753. *Gen. Pl.*, ed. 5: 470. 1754.

Decumbent or caespitose [rhizomatous or stoloniferous] perennials or annuals. Stems 10–200 cm high, often branched, from tuberous or non-tuberous bases; nodes solid or spongy; nodes glabrous. Leaves with sheaths glabrous or pubescent; ligule a fringed membrane or a fringe of hairs; blades linear, flat or folded, glabrous to scabrous or pubescent, with cuneate or truncate bases, rolled in bud; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences spike-like, with clusters of spikelets on highly reduced axes. Spikelets dorsiventrally compressed, sessile, borne in small clusters of 1–4 [–8] subtended by involucre of basally connate, often flattened, spiny bristles (reduced secondary branches), the spiny unit being dispersed as a whole; proximal florets staminate or sterile, paleate. Calli flared to form discoid receptacle. Glumes 1 or 2, unequal, awnless, 1–7 nerved. Proximal lemmas equal to distal lemmas, awnless, 3–7 nerved; distal lemmas chartaceous to cartilaginous, glabrous to scabrous, smooth to muricate, yellow to green, dull, acute to acuminate, 3–7 nerved, with flat margins and conspicuous germination flap. Distal paleas equalling and similar in texture to distal lemmas, awnless, 2 nerved. Lodicules absent. Ovaries with styles fused at base or free. Caryopses (grains) smooth; endosperm hard, without lipid, containing only simple starch grains. Base chromosome numbers 9, 17. (Including *Cenchropsis* Nash.) LECTOTYPE SPECIES: *Cenchrus echinatus* L.; see Nash, in Britton & Brown, *Illus. Fl. No. U.S. & Canada*, ed. 2, **1**: 166. 1913. (Name from Greek, *kenchros*, the name of a small millet used by the ancient Greeks.) — SANDBUR, SANDSPUR, BURGRASS, HEDGEHOG GRASS, DEVIL'S BURS.

A circumtropical genus of 20 species, with some species occurring in the temperate zones of the Northern and Southern Hemispheres, in wet or dry grasslands, fields, shores, dunes, open woodlands, and disturbed sites. DeLisle (1963) recognized two groups of species within *Cenchrus* but did not treat them formally. The more specialized group, to which all of the native North American species belong, is characterized by "burs" (in which the spines are flattened and conspicuously connate)

and by the base chromosome number 17. The less specialized group contains species with less connate spines (in certain species, some of the spines may be free to the base of the involucre) and with base numbers of 9, 10, or 17. All but one species in the second group are native to the Old World.

Seven species of *Cenchrus* are native in North America, and all occur in the Southeast. In addition, two species, *C. ciliaris* L. and *C. setigerus* Vahl, have been introduced into North America; *C. setigerus* occurs in our area. One other species, *C. Palmeri* Vasey, a native of Baja California and northwestern Mexico, is known from places near the United States border; it may occur in extreme southern California and/or southwestern Arizona.

Cenchrus Brownii Roem. & Schultes (single whorl of united, retro-sor-sely barbed spines, subtended by equal or longer, finer bristles; burs crowded; peduncles ca. 2 mm wide; $2n = 34, 36$, ca. 66, $n = 34$) occurs from Texas and extreme southern Florida (Keys) through the West Indies and Central America to Brazil and Bolivia. It was introduced into Australia, and has become an adventive in parts of Southeast Asia, the Philippines, certain Pacific islands, and South Africa (DeLisle, 1963).

Cenchrus echinatus, southern sandspur (similar to *C. Brownii*, but with bristles shorter than spines, less crowded inflorescences, peduncles more than 2 mm wide), $2n = 34, 68$, $n = 34$, occurs from California, Arizona, Texas, and the District of Columbia south to Argentina and Chile. It is an adventive in the Hawaiian Islands and on other Pacific islands, Australia, the Philippines, Israel, and probably elsewhere.

Cenchrus gracillimus Nash, slender sandspur (perennial; leaves usually less than 3 mm wide and more than 3 cm long, flat; several series of flattened spines on surface of bur), $n = 17$, is restricted to the Southeast (Georgia, Florida, Alabama) and the West Indies. It forms dense matted clumps, unlike any other North American species. Its burs are nearly glabrous and have long, narrow spines.

Cenchrus longispinus (Hackel) Fern. (annual; leaves more than 3 mm wide; burs 6–18, with numerous (usually more than 50), slender spines usually less than 7 mm long), $n = 17$, $2n = 34, 36$, is the most widespread *Cenchrus* in North America, extending from Massachusetts to Ontario and North Dakota, south to Florida and California, with a few stations in Oregon. It is also scattered in Central America and the West Indies, and has become naturalized in Europe, South Africa, and Australia. DeLisle (1963) considered it to be invasive in the western portion of its range in the United States. This species has been called *C. pauciflorus* Benthham in several North American floras, but that name actually applies to *C. incertus* M. A. Curtis (DeLisle, 1963). One chromosome count, $2n = 36$ (Brown, 1948; sub *C. pauciflorus*), is anomalous; all other determinations from throughout the range of *C. longispinus* (plants from Kansas, New Mexico, Colorado, Nebraska, California, Texas) are $n = 17$ ($2n = 34$).

Cenchrus tribuloides L., dune sandbur (annual; leaves more than 3 mm wide; burs densely pubescent; spines broad at base, fewer than 45;

spikelets usually solitary, 6–9 mm long), $2n = 34$, $n = 17$, is restricted to coastal areas of the Atlantic Seaboard, the eastern Gulf of Mexico, Bermuda, and the Bahamas. In the Southeast it is known from North Carolina, South Carolina, Georgia, Florida, Mississippi and Louisiana. *Cenchrus tribuloides* has the largest and most densely pubescent burs of any species in the genus. Some plants in southern Florida do not have the long hairs typical of the species, but in these the burs are large and covered with dense, short pubescence.

Cenchrus incertus, fine-bristled burgrass, coast sandspur (similar to *C. tribuloides* but burs glabrous to short-pubescent; spikelets 2–4, each less than 6 mm long), $2n = 34$, $n = 16, 17$, is widespread, extending from Virginia to Arizona and southern California, southward through Central America to Panama and also in the West Indies. It is also native to South America, from southern Peru and southern Brazil to northern Chile, northern Argentina, and Uruguay. It is naturalized in the Philippines and in South Africa, where it is considered a noxious weed (DeLisle, 1963). Its fruits often occur in bird-seed mixtures, with those of the millets. It is a rare weed in Britain (Hanson & Mason).

Some West Indian plants have burs with more hairs and more robust stems than is usual for *Cenchrus incertus*. These have been considered to belong to *C. tribuloides*. However, DeLisle (1963) included them within *C. incertus* because they usually have two or three spikelets per bur, and the burs are smaller than those of typical *C. tribuloides*. *Cenchrus pauciflorus*, assigned to *C. longispinus* in various North American floras, actually is a synonym of *C. incertus*. Measurements of bur width, spine number, rachis internode length, and leaf length from the type specimen of *C. pauciflorus* fall well within the limits for these characters in *C. incertus* (DeLisle, 1963).

Cenchrus myosuroides Kunth (perennial; burs densely crowded; spines terete, glabrous, connate only at base of bur, none prolonged beyond bur, $2n = 54$, ca. 68, 70) grows in southern Texas, southern Louisiana, and extreme southern Florida in the United States. It also occurs from Mexico to northern Argentina and southern Brazil, and is also known in the West Indies. Nash (1903) proposed *Cenchropsis* for *C. myosuroides*, but he later merged it with *Cenchrus* (Nash, 1909). Variation in degree of spine fusion within *Cenchrus* is continuous; thus, removal of *C. myosuroides* (and other species such as *C. ciliaris*) is arbitrary.

Two exotic species that have been cultivated in the Southeast, *Cenchrus ciliaris* and *C. setigerus*, have spines that are connate only at the base, as in *C. myosuroides*. *Cenchrus ciliaris*, buffelgrass, is a native of Africa and India. It is an adventive in Texas, Mexico, South America, and Australia, and has been cultivated in Florida. It is a good forage grass in dry areas. Different chromosome numbers have been reported for *C. ciliaris* ($2n = 32, 34, 36, 38, 40, 44, 45, 52, 54$; $n = 18$), and meiotic irregularities in most of the aneuploids suggest the occurrence of apomictic reproductive mechanisms. *Cenchrus setigerus*, birdwood grass, is native to an area similar to that of *C. ciliaris*. It

has been introduced into the southern United States (Florida, Mississippi, Louisiana, Texas), and also into South America and Australia. It differs from *C. ciliaris* in having short, glabrous spines, none of which is prolonged beyond the bur. It contains apomictic populations. Chromosome numbers reported from *C. setigerus* are $2n = 34, 36, 37$ and $n = 17$ and 18 . Meiosis is regular in plants of *C. ciliaris* and *C. setigerus* with $2n = 36$. However, in aneuploids and polyploids of both species, lagging chromosomes are common at anaphase-I (Fisher *et al.*). Apomictic reproduction was shown in both species by Fisher *et al.*, who found that seed set in bagged inflorescences always approached that of normal open-pollinated inflorescences. The meiotic products in the ovules usually degenerate soon after formation, and one or more cells of the nucellus enlarge to become unreduced embryo sacs (apospory). Pollination is necessary to initiate endosperm division, which precedes division of the unfertilized egg (Snyder *et al.*, 1955a, b). In controlled crosses between these species (sexual plants of *C. ciliaris* and apomictic plants of *C. setigerus*), it was found that apomixis in *C. ciliaris* may have been facultative. Progeny produced by selfing or crossing with *C. setigerus* are more uniform morphologically than are those from fully sexual plants. The entire spectrum of reproductive behavior, from the obligate sexual state to obligate apomixis, is found in *C. ciliaris* (Bray).

Cenchrus is most closely related to *Pennisetum* (Clayton & Renvoize). Distinctions between these genera have not been well defined until recently. Although the degree of fusion of bristles in most New World species of *Cenchrus* is substantial (and as a result, their burs do not resemble the fascicles of bristles subtending the spikelets of *Pennisetum* species), there are several Old World species of *Cenchrus* in which the distinction is less obvious. As generally circumscribed, *Cenchrus* contains species in which the bristles are to some degree fused into a cup-like structure or bur, whereas the bristles of *Pennisetum* are free. In *C. ciliaris* the degree of fusion is limited, and this species has often been placed in *Pennisetum*. *Cenchrus ciliaris* has one bristle longer than the others, and this feature has been interpreted as an extension of the fascicle axis (Sohns, 1955). However, in *C. ciliaris* the vascular system of the long bristle seems to arise from the same level as that of the shorter bristles, whereas in *Pennisetum*, the vascular system of the prolonged fascicle axis arises from a level above the vascular bundles of the involucral bristles. Thus, it appears that the transfer of *C. ciliaris* to *Pennisetum* is unwarranted.

Webster (1987, 1988) found callus morphology to reliably separate *Cenchrus* and *Pennisetum*. In *Cenchrus* the callus is flared or swollen at the apex, but in *Pennisetum* the callus is unmodified.

DeLisle (1963) suggested that *Cenchrus* may have originated in Africa or India because of the preponderance of relatively unmodified species in those areas, and because of the presence there of the closely related genus *Pennisetum*.

The burs of *Cenchrus* are clearly designed for dispersal through adhesion to fur. In *C. tribuloides* (and other species) each spine has barbs on its surface, particularly near the apex. These barbs are retrorsely directed in most species. The burs, when attached to clothing (and presumably to fur), work themselves inward toward the skin, and can inflict painful wounds. The pain and duration of these wounds may be exacerbated by a substance of unknown composition contained within the barbs (Gayle).

REFERENCES:

- Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; BROWN (1948); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE & POHL (1974); GOULD (1975); HANSON & MASON; JONES & COILE; MACROBERTS; NASH (1903, 1909); POHL (1980); RADFORD *et al.*; SHINNERS (1954); E. SMITH; SOHNS (1955); TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.
- BASHAW, E. C. Apomixis and sexuality in buffelgrass. *Crop Sci. Madison* **2**: 412–415. 1962. [Some plants of *C. ciliaris* reproduce sexually; the majority are apomicts.]
- BRAY, R. A. Evidence for facultative apomixis in *Cenchrus ciliaris*. *Euphytica* **27**: 801–804. 1978.
- CARO, J. A., & E. SANCHEZ. Notas criticas sobre especies de *Cenchrus* (Gramineae). *Kurtziana* **4**: 39–50. 1967a. [Four spp.]
- & ———. Las especies de *Cenchrus* (Gramineae) de la Republica Argentina. *Ibid.* 95–129. 1967b. [Five spp.; recognizes subg. *Cenchropsis* (Nash) Caro & Sanchez; illustrations of several species.]
- CHASE, A. The North American species of *Cenchrus*. *Contr. U.S. Natl. Herb.* **22**: 45–77. 1920. [Ten spp.]
- DELISLE, D. G. Taxonomy and distribution of the genus *Cenchrus*. *Iowa State Jour. Sci.* **37**: 259–351. 1963. [Best available monograph; detailed descriptions and discussions, distribution maps, illustrations, specimen citations.]
- . Chromosome numbers in *Cenchrus* (Gramineae). *Am. Jour. Bot.* **51**: 1133, 1134. 1964. [Six spp.]
- FARODA, A. S., & P. S. TOMER. *Cenchrus ciliaris*—a perennial pasture grass of arid and semi-arid areas. *Indian Forester* **97**: 675–680. 1971.
- FISHER, W. D., E. C. BASHAW, & E. C. HOLT. Evidence for apomixis in *Pennisetum ciliare* and *Cenchrus setigerus*. *Agron. Jour.* **46**: 401–404. 1954. [Both now treated as species of *Cenchrus*.]
- GAYLE, E. E. The spines of *Cenchrus tribuloides* L. *Bot. Gaz.* **17**: 126, 127. 1892.
- HERNANDEZ, A. R. DE. Observations on the chromosome number of *Pennisetum ciliare*. *Jour. Agr. Univ. Puerto Rico* **37**: 161–170. 1953. [= *C. ciliaris*; $2n = 36, 54$.]
- HODGKINSON, K. C., M. M. LUDLOW, J. J. MOTT, & Z. BARUCH. Comparative responses of the savannagrasses *Cenchrus ciliaris* and *Themeda triandra* to defoliation. *Oecologia* **79**: 45–52. 1989. [*C. ciliaris* tolerant of heavy grazing.]
- JOHNSTON, M. C. *Cenchrus longisetus* M. C. Johnston, nōm. nov. (Gramineae). *Sida* **1**: 182. 1963. [An unjustified name change and transfer for a species of *Pennisetum*.]
- LEA, A. M. An insect-catching grass (*Cenchrus australis* R. Br.). *Trans. Proc. Roy. Soc. S. Austral.* **39**: 92, 93. 1915. [Many insects of diverse orders caught on the retrorse barbs of bur bristles.]
- MILLER, E. V., A. E. MILLER, & E. MESIANO. Effect of maleic hydrazide on growth and reproduction of the sandbur. *Bot. Gaz.* **117**: 76–78. 1955. [Seed germination within burs is not necessarily simultaneous but may be sequential.]

- NASH, G. V. The genus *Cenchrus* in North America. Bull. Torrey Bot. Club **22**: 298–302. 1895. [*C. tribuloides* mistaken for the widespread *C. longispinus*.]
- PERIS, J. B., F. ESTESO, & R. ROSELLÓ. *Cenchrus ciliaris* L., un neófito de óptimo Saharo-Sindiano nuevo para la flora Iberica. Anal. Jard. Bot. Madrid **44**: 176. 1987.
- PONNAIYA, B. W. X., V. S. RAMAN, & D. R. JAGANNATH. Two new chromosomal races in the genus *Cenchrus* Linn. Sci. Cult. **32**: 195, 196. 1966. [Apomixis inferred in *C. ciliaris* and *C. setigerus* on the basis of meiotic irregularities and low pollen fertility.]
- READ, J. C., & E. C. BASHAW. Cytotaxonomic relationships and the role of apomixis in buffelgrass and birdwoodgrass. Crop Sci. Madison **9**: 805, 806. 1969. [*C. ciliaris*, *C. setigerus*.]
- RUNYON, H. E. A new sandbur from western Oklahoma: *Cenchrus Albertsonii*. Am. Jour. Bot. **26**: 485, 486. 1939. [Perennial.]
- SHINNERS, L. H. *Cenchrus parviceps* (Gramineae), a new species from southern Texas. Field Lab. **24**: 73, 74. 1956.
- SNYDER, L. A., A. R. HERNANDEZ, & H. E. WARMKE. The mechanism of apomixis in *Pennisetum ciliare*. Jour. Agr. Univ. Puerto Rico **39**: 150–164. 1955a. [= *C. ciliaris*.]
- , & ———. The mechanism of apomixis in *Pennisetum ciliare*. Bot. Gaz. **116**: 209–221. 1955b. [= *C. ciliaris*.]
- TALIAFERRO, C. M., & E. C. BASHAW. Inheritance and control of obligate apomixis in breeding buffelgrass, *Pennisetum ciliare*. Crop Sci. Madison **6**: 473–476. 1966. [= *C. ciliaris*; origin of asexually reproducing plant through mutation at one locus; but unclear why the sexual condition is derived.]

5. *Anthephora* Schreber, Besch. Gräser **2**: 105. pl. 44. 1779.

Caespitose or decumbent [rhizomatous or stoloniferous] annuals [perennials]. Stems 15–150 cm high, branched or unbranched; internodes hollow; nodes glabrous or sparsely pubescent. Leaves with sheaths pubescent; ligule an unfringed [fringed] membrane; blades linear [lanceolate], flat [folded], pubescent, with truncate bases, rolled in bud; photosynthesis C_4 , biochemical pathway NADP-me. Inflorescences spike-like, disarticulating at maturity. Spikelet fascicles short-pedicellate, erect, subtended by distinctly flattened, free, involucre bristles, the entire fascicle-bristle unit disarticulating at maturity; outer spikelet of each fascicle staminate, subtended by a broad, indurate, acute, 11–15 nerved bract. Spikelets dorsiventrally compressed, adaxial, sessile, in fascicles of [2–] 4 [–11]; proximal florets sterile, epaleate. Calli prolonged into a stipe, flared at apex and fused to bracts. Glumes 1, setaceous, pubescent along margins, 1 nerved. Proximal lemmas membranaceous, pubescent, 2–7 nerved; distal lemmas chartaceous, smooth, glabrous, acute, with margins flat, thin, enclosing palea, and with [without] conspicuous germination flap. Distal paleas 2 nerved. Lodicules 0. Ovaries with styles fused or free, stigmas brown. Caryopses (grains) with endosperm hard, lacking lipid, with simple starch grains. Chromosome base number 9. TYPE SPECIES: *Anthephora elegans* Schreber = *A. hermaphrodita* (L.) Kuntze, the only species included in the genus at the time of its original description. (Name from Greek *anthos*, flower, and *phoreus*, a bearer.)

A genus of about 12 species of African tropical grasslands and savannahs, with one species, *A. hermaphrodita* (L.) Kuntze, a widespread weed in the Neotropics. *Antheophora hermaphrodita* was introduced into Florida early in the 20th century and escaped from cultivation, but it may not now occur in North America (Webster, 1988). Hall noted it as being rare in Florida, escaped from cultivation in Alachua County, but he did not indicate when this occurred.

Antheophora is a bizarre genus within tribe Paniceae. There has been considerable debate over the interpretation of spikelet (and fascicle) structure. Many authors have considered the indurate bracts subtending the spikelet clusters to be partially fused glumes. Bentham, Hackel, Nash (1909), Bews, Avdulov, and Roshevits treated *Antheophora* as a member of the tribe Zoysieae (= Cynodonteae Dumort.), now included in subfamily Chloridoideae. Avdulov qualified his treatment by saying that the tribe, as then defined, was not a natural assemblage. Some authors have preferred to place it in a monotypic tribe Anthephoreae Pilger ex Potztal (Connor, 1981; De Wet & Anderson; Pilger, 1954) or subtribe Anthephorinae Pilger (Pilger, 1940). Other authors, despite their misinterpretations of fascicle and spikelet structure, retained *Antheophora* in tribe Paniceae (e.g., Chippindall; Clayton & Renvoize; Reeder, 1960). It is placed with other genera that have modified involucre, such as *Cenchrus* and *Pennisetum*, in subtribe Cenchrinae or its equivalent (Clayton & Renvoize; Reeder, 1960; Stapf, 1917-1930). Species of *Antheophora* have typical panicoid embryos, microhairs, silica bodies, and leaf anatomy, unlike those of tribe Zoysieae (Reeder, 1957, 1960).

Antheophora pubescens Nees has 4-nucleate embryo sacs (vs. 8-nucleate), a condition correlated with somatic apospory (Brown & Emery, 1958; Connor, 1981). Aneuploidy may also have occurred in the genus. Plants of *A. hermaphrodita* from throughout its range have nine sets of chromosomes (four Mexican locations and one in Costa Rica); those of *A. argentea* Goossens also have $n = 9$ (Cape Province of South Africa). However, *A. pubescens* has $2n = 40$ in the Transvaal of South Africa, indicating a base number of 10 (De Wet & Anderson). There is some question about the validity of this last count because Spies found $2n = 36$ in all five samples studied by him. On the basis of chromosomal associations at meiosis, he concluded that *A. pubescens* was probably a segmental allotetraploid.

The mode of dispersal in *Antheophora* is presumably through adhesion of the 'bur' (fascicle of spikelets with subtending bracts) to the fur of mammals (Davidse, 1987).

REFERENCES:

- Under references for tribe see AVDULOV; BENTHAM; BEWS; BOLKHOVSKIKH *et al.*; BROWN & EMERY (1958); CHIPPINDALL; CLAYTON & RENVOIZE; CONNOR (1981); DAVIDSE (1987); DE WET & ANDERSON; HACKEL; HALL; NASH (1909); PILGER (1940, 1954); POHL (1980); REEDER (1957); ROSHEVITS; STAPF (1917-1930); WATSON & DALLWITZ; and WEBSTER (1988).

- REEDER, J. R. The systematic position of the grass genus *Antheophora*. Trans. Am. Microscop. Soc. 79: 211–218. 1960. [Interprets structures subtending spikelet fascicles as modified glumes of sterile spikelets, but nevertheless considers *Antheophora* to be a member of the tribe Paniceae, not Zoysieae.]
- SPIES, J. J. The ploidy status of *Antheophora pubescens* (Panicoideae). S. Afr. Jour. Bot. 1: 77. 1982. [Five cultivars were tetraploid, $2n = 36$; chromosome number ($2n = 40$) reported by De Wet & Anderson likely incorrect.]

Subtribe SETARIINAE (Dumortier) Dumortier, Fl. Belg. 149. 1827.⁷

6. *Oplismenus* Palisot de Beauvois, Fl. Oware 2: 14. 1810, nom. cons.

Decumbent or stoloniferous perennials [annuals]. Stems 5–60 [100] cm high; internodes solid or spongy; nodes pubescent. Leaves with sheaths pubescent; ligule a fringed membrane or a fringe of hairs; blades linear to ovate, flat, pubescent, with rounded bases, pseudopetiolate or not, with readily visible transverse veins, rolled in bud; photosynthesis C_3 . Inflorescences paniculate, open, with a central axis and 3–8 spreading, spike-like, secund primary branches terminating in spikelets; secondary branches, if present, sometimes reduced to fascicles of spikelets. Spikelets laterally to dorsiventrally compressed, disarticulating below the glumes, abaxial, secund, short-pedicellate (pedicel apices discoid), solitary or paired, biseriate; proximal florets sterile (sometimes staminate), paleate (palea may be vestigial). Calli hairy, undifferentiated. Glumes 2, nearly equal, shorter than lemmas, one or both awned, awns viscid [scabrous]; proximal glumes membranaceous, pubescent, 3–5 nerved; distal glumes membranaceous, pubescent, 5–7 nerved. Proximal lemmas exceeding distal lemmas, membranaceous, pubescent, acute to short-awned, 5–7 [9] nerved; distal lemmas elliptic, cartilaginous, smooth, lustrous, glabrous, white to yellow, acute to mucronate, 3–5 nerved, with recurved apex, involute margins and conspicuous germination flap. Distal paleas cartilaginous, awnless, 2 nerved. Lodicules 2. Ovaries with styles free. Caryopses (grains) with endosperm hard, lacking lipid, containing only simple starch grains. Chromosome base numbers 9, 10, 11. TYPE SPECIES: *Oplismenus africanus* Beauv. = *O. hirtellus* (L.) Beauv., the only species included in the genus at the time of its original description. (Name from Greek, *hoplismenos*, armed, in reference to the long awns of the spikelets.) — WOODGRASS, BASKETGRASS, RIBBONGRASS.

A genus of five to nine species of moist forests and wooded flood-plains of the tropical and subtropical regions of the world (Davey & Clayton; U. Scholz). The awned proximal glume, alternating secund inflorescence branches, and creeping growth habit distinguish *Oplismenus* from other Paniceae.

There has been considerable difference of opinion over species limits in this genus. *Oplismenus hirtellus* and *O. setarius* (Lam.) Roemer

⁷Dumortier did not use the rank of subtribe until 1827.

& Schultes have been reported from the Southeast, but they are not distinct (Davey & Clayton, U. Scholz). Hall has noted that some specimens from southern Florida approach *O. hirtellus* in the strict sense. However, there are other plants in which one flowering stem will resemble *O. hirtellus* and another *O. setarius*. When material from around the world is considered, the most sensible treatment of the variation in this complex results in the recognition of one polymorphic species, *O. hirtellus*. In North America, *O. hirtellus*, $2n = 72$, occurs from coastal North Carolina southward throughout Florida, and west to Arkansas and Texas.

Davey & Clayton treat the *Oplismenus compositus* (L.) Beauv. complex, a circumtropical group, as a polymorphic species as well, although U. Scholz prefers to maintain *O. aemulus* (R. Br.) Roemer & Schultes as a distinct species in this group. The morphometric analyses of Davey & Clayton showed that five species could be distinguished among the polymorphic complexes, but even some of these appear to intergrade (Webster, 1987).

Two sections within the genus, sect. *Oplismenus* and sect. *Scabriseta* Schlecht., were recognized by U. Scholz. Section *Oplismenus* (awns coarse, smooth, reddish to yellowish, usually viscid) contains *O. aemulus*, *O. hirtellus*, and *O. compositus*. Sect. *Scabriseta* (awns delicate, scabrous, whitish, not viscid) contains *O. affinis* Schultes, *O. Baroni* A. Camus, *O. Burmannii* (Retz.) Beauv., *O. flavicomus* Mez, *O. gracillimus* Mez, and *O. Humbertianus* A. Camus. All but *O. affinis* and *O. Burmannii* are endemic to Madagascar.

The relationships of *Oplismenus* within the Paniceae are uncertain. Webster (1988) has suggested *Ichnanthus* Beauv. and *Panicum* as possible close relatives. Clayton & Renvoize have placed *Oplismenus*, along with *Poecilostachys* Hackel, *Ichnanthus*, and several other small tropical genera, on a line diverging from near the base of *Panicum*. The method by which their diagram of relationships was derived is not indicated, although leaf anatomical patterns are included. *Acroceras* Stapf, *Commelinidium* Stapf, *Ichnanthus*, and *Cyrtococcum* Stapf are most similar to *Oplismenus* in Watson & Dallwitz's phenetic analysis. Pohl (1980) has noted that *Oplismenus* superficially resembles *Pseudechinolaena* Stapf in growth habit and *Echinochloa* in spikelet structure. *Oplismenus* has been placed in subtribe Microcalaminae (Butzin, 1970) along with other genera that have forest or shade adaptations.

Most chromosome counts in *Oplismenus* are based on $x = 9$, with diploid to decaploid levels being documented, and a wide range of ploidy levels occurring even within a single species (e.g., *O. Burmannii*; Mitra & Datta; Khosla & Singh). Different base numbers have been reported occasionally; for example, $x = 11$ ($2n = 44$, also in *O. Burmannii*, Mehra & Chaudhary, 1975), and $x = 10$ ($n = 10$, *O. compositus*, Sharma & Kumar; $2n = 60$, *O. hirtellus*, De Wet, 1958). Seed set is poor in some species of *Oplismenus*, due to degeneration of megaspore tetrads or the female gametophyte at various stages of development (Bhanwra). No

attempt appears to have been made to search for a correlation between such degeneration and ploidy level.

Species of *Oplismenus* are characteristic components of tropical forest floors and often form large, tangled colonies (Chippindall). The awns are either scabrous or viscid and provide a means of seed dispersal through adhesion (Clayton & Renvoize; Davidse, 1987).

Oplismenus hirtellus is a common constituent of commercial bird food mixtures (Hanson & Mason). It has been used to treat toothaches in northwestern Venezuela. A form with variegated leaves is woven into baskets in Trinidad. The species is also grown as an ornamental in gardens and greenhouses (Morton; Roshevits). Several species are weeds of tea plantations and other commercial operations in the tropics (Holm *et al.*; Roshevits).

REFERENCES:

- Under references for tribe see BHANWRA; BLOMQUIST; BOLKHOVSKIKH *et al.*; BUTZIN (1970); CHASE (1911); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); DE WET (1958); GOULD (1975); HALL; HANSON & MASON; HOLM *et al.*; JONES & COILE; MACROBERTS; MORTON; POHL (1980); RADFORD *et al.*; ROSHEVITS; E. SMITH; TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.
- DAVEY, J. C., & W. D. CLAYTON. Some multiple discriminant function studies on *Oplismenus* (Gramineae). Kew Bull. **33**: 147–157. 1978. [Number of species recognized reduced from nine to five based on analysis of worldwide patterns of variation.]
- HITCHCOCK, A. S. The North American species of *Oplismenus*. Contr. U.S. Natl. Herb. **22**: 123–132. 1920. [Four species in the American tropics; only *O. setarius* (= *O. hirtellus*) in the United States.]
- MORRIS, M. W. Noteworthy vascular plants from Grenada County, Mississippi. Sida **13**: 177–186. 1988. [*O. setarius* (= *O. hirtellus*).]
- SCHLECHTENDAL, D. F. L. VON. Betrachtungen über *Hoplismenus*. Linnaea **31**: 263–313. 1861. [Early worldwide revision; discusses each name under the genus in which it was originally described; thus, no new combinations made.]
- SCHOLZ, U. Monographie der Gattung *Oplismenus* (Gramineae). Phanerogam. Monogr. **13**. 213 pp. 1981. [A more detailed monograph than that of DAVEY & CLAYTON, with detailed descriptions, range maps, and excellent illustrations of all species.]

7. *Panicum* Linnaeus, Sp. Pl. **1**: 55. 1753; Gen. Pl. ed. 5: 29. 1754.

Rhizomatous, decumbent, or caespitose perennials or annuals. Stems 20–400 cm high, herbaceous [woody], branched or unbranched, from tuberous or non-tuberous bases; internodes solid, spongy, or hollow, sometimes viscid; nodes glabrous or pubescent. Leaves cauline and/or basal (basal leaves often differentiated and forming a rosette in most species of subgenus *Dichanthelium*), with sheaths pubescent or glabrous (sheath apices broadly auriculate in *P. abscissum*); ligule a fringed or unfringed membrane, a fringe of hairs, or absent; blades linear to lanceolate, flat, folded or involute, glabrous or pubescent, margins sometimes cartilaginous and white, with cuneate to rounded bases,

rolled in bud; photosynthesis C_3 or C_4 , biochemical pathway NAD-me, or NADP-me. Inflorescences paniculate, open or contracted, with glabrous, pubescent, or glandular branches terminating in spikelets. Spikelets elliptic, lanceolate, or obovate, sometimes anthocyanic, dorsiventrally or laterally compressed, disarticulating below the glumes (or not at all when entire inflorescences are dispersed as a unit), adaxial, sometimes second, pedicellate (pedicel apices cupuliform, sometimes finely pubescent), solitary or paired; proximal florets staminate or sterile, paleate or epaleate; rachilla pronounced or not between glumes and/or florets. Calli undifferentiated. Glumes 2, equal or unequal, glabrous or pubescent, obtuse to acute, awnless; proximal glumes often shorter than distal glumes, 0–7 nerved, encircling spikelet base; distal glumes similar to proximal lemmas in size (sometimes slightly longer) and texture, smooth to muricate, obtuse to acuminate, sometimes narrowed and laterally flattened at apex, 3–11 [–15] nerved. Proximal lemmas less firm than distal lemmas, glabrous or pubescent, obtuse to acuminate, awnless, 3–11 nerved; distal lemmas cartilaginous, smooth to muricate, glabrous (rarely pubescent at apex), acute or obtuse, awnless, 3–11 nerved, with involute margins and a conspicuous germination flap. Distal paleas indurate, awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red or brown. Caryopses (grains) small, not grooved, smooth; pericarp thin; endosperm hard, without lipid, with simple and/or compound starch grains. Base chromosome numbers 9, 10. (Including *Dichanthelium* (Hitchc. & Chase) Gould, *Phanopyrum* (Raf.) Nash, *Steinchisma* Raf.). LECTOTYPE SPECIES: *Panicum miliaceum* L.; see Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 14. 1910. (Name Latin, an old name for millet.) — PANIC GRASS, PANICUM, SWITCHGRASS, MAIDENCANE, MILLET, TORPEDO GRASS, CUTTHROAT GRASS, BEACHGRASS.

A genus of more than 500 species, occurring in virtually all types of habitats, from wet or dry woodlands, grasslands, shores, and marshes, to disturbed areas and cultivated fields, principally throughout the tropics of the world, but with many species in the Temperate Zone of North America. *Panicum* is one of the largest genera of angiosperms. It accounts for nearly a quarter of the species in the Paniceae (Webster, 1988).

Early treatments of *Panicum* tended to be very inclusive (e.g., Bentham; Hackel). Some of the segregates described since then have withstood the test of time, but others have not, and realignments continue to the present. For example, *Yakirra* Lazarides & R. Webster was proposed for Australian species with swollen rachilla internodes between the glumes, hairy distal-glume and proximal-lemma apices, and smooth surfaces on the distal floret (Berg; Lazarides, 1959; Lazarides & Webster; Webster, 1987). A group of species centered around *P. maximum* Jacq., Guinea grass, (*P. subg. Megathyrsus* Pilger) has several unusual character states, including PEP-ck decarboxylation and transversely rugose distal floret-bracts with simple papillae on the wrinkles. These

character states recall *Urochloa*, and Webster (1987) recently made the transfers, supporting Hsu's suggestion (1965) to remove subg. *Megathyrsus* from *Panicum*. Several groups that had been included in *Panicum* by Hitchcock & Chase (1910) have also been transferred elsewhere in the light of new evidence from anatomy, cytology, physiology, and biochemistry, e.g., subg. *Paurochaetium* Hitchc. & Chase, which is now in *Setaria* Beauv., the Geminata group, which is in *Paspalidium* Stapf, and the Fasciculata and Purpurascens groups, which are in *Urochloa*. Zuloaga & Soderstrom also contributed to the streamlining of *Panicum* by removing clearly disparate elements and providing detailed justifications for doing so. Their transfers generally involve Neotropical species that belong in *Brachiaria* (= *Urochloa*, in large part), *Homolepis* Chase, *Ichnanthus*, *Paspalum*, *Streptostachys* Desv. emend. Zuloaga & Soderstrom, and *Tatianyr* Zuloaga & Soderstrom.

Panicum is at the center of a complex of related genera (Clayton & Renvoize; Hsu, 1965). Many of the groups here treated as subgenera (*Dichanthelium*, *Phanopyrum*, *Steinchisma*) would probably render *Panicum* paraphyletic if they were recognized as distinct genera. Other close relatives appear to have apomorphies that justify their recognition as genera (e.g., *Eriochloa*, *Hymenachne*, *Lasiacis*, *Paspalidium*, *Sacciolepis*, and *Urochloa* in our area). Unfortunately, no phylogenetic analysis of *Panicum* and its relatives has been undertaken. It is clear that the genera listed above, as well as *Amphicarpum* and *Acroceras* Stapf, belong to this complex. Hsu (1965) considered *Lasiacis* to be ancestral to *Panicum*, as did Davidse (1978).⁸ Watson & Dallwitz indicate that *Tricholaena* Schrader ex Schultes (usually placed with *Melinis* in subtribe Melinidinae), *Leucophrys* Rendle (a segregate of *Urochloa*), and *Anthaenantia* are also similar to *Panicum* phenetically, although this does not necessarily imply a close phylogenetic relationship. Clayton & Renvoize also note the similarity between *Tricholaena* and *Panicum*, and *Ancistrachne* S. T. Blake, *Cyrtococcum* Stapf, *Homolepis*, *Hylebates* Chippindall (in subtribe Digitariinae), *Ichnanthus*, *Whiteochloa* C. E. Hubb., and *Yakirra* are also allied genera. Butzin (1970) placed *Leptoloma* with *Panicum* in his emended subtribe Panicinae, but the former is clearly part of *Digitaria*. This is a complex issue, and little of substance can be contributed to a discussion of the relationships of *Panicum* until explicit analyses have been made.

Panicum is fairly uniform in spikelet morphology, but very diverse in vegetative features, habit, and pubescence characters. Various schemes have been proposed to deal with this variation. The most useful recent treatment of the New World representatives of the genus is that of Zuloaga (1987a), and his infrageneric classification is, for the most part, followed here. His treatment contains some innovations, but it also incorporates many of the ideas of Hsu (1965) and Hitchcock & Chase (1910).

⁸See *Lasiacis* (Griseb.) Hitchc., genus 8 in this treatment.

In the southeastern United States, *Panicum* is represented by five subgenera: *Panicum*, *Agrostoides* (Hitchc.) Zuloaga, *Phanopyrum* (Raf.) Pilger, *Dichantherium* Hitchc. & Chase, and *Steinchisma* (Raf.) Zuloaga.

Subgenus PANICUM contains species with the C_4 photosynthetic pathway and the NAD-me decarboxylation system. Major vascular bundles in the leaves are enclosed in two sheaths, an inner mestome sheath of thick-walled cells and an outer sheath with cells containing (usually) centripetally arranged chloroplasts. The inflorescences are generally large, lax, and diffuse. The spikelets tend to be ellipsoid to lanceolate, with the distal lemma and palea mostly smooth, glabrous, and lustrous. Compound, rounded papillae are present near the apex of the palea. The base chromosome number of species in subg. *Panicum* is $x = 9$. New World members of subg. *Panicum* are distributed in five sections; sections *Panicum*, *Dichotomiflora* (Hitchc. & Chase) Honda, and *Repentia* Stapf are represented by one or more species in the Southeast. Section PANICUM (proximal glumes long, $1/2$ to $3/4$ the length of the spikelet, 5–7 nerved) contains several widespread, weedy species, such as *P. miliaceum*, proso millet, and *P. capillare* L., common witchgrass, and its close relatives. Section DICHOTOMIFLORA (proximal glumes short, $1/5$ to $1/3$ of spikelet length, 1–3 nerved), includes *P. dichotomiflorum* Michx. var. *dichotomiflorum*, fall panicum (foliage glabrous), and var. *bartowense* (Scribner & Merr.) Fern. (foliage pubescent). Although *P. dichotomiflorum* and its relatives have been characterized as NAD-me subtype C_4 species, their leaf anatomy is variable, with some species having centrifugally arranged chloroplasts in the bundle sheath cells, and other species having them arranged centripetally (Ohsugi & Murata, 1980, 1986). In fact, the difference in the disposition of chloroplasts within bundle sheath cells is even found *within* a species in this section, *P. coloratum* L., in which Kabulabula and Solai (two cultivars) have the centrifugal arrangement, and two varieties (var. *coloratum*, var. *makarikariense* Goossens) have the centripetal arrangement. Ohsugi & Murata (1986) speculate that such variability within the section and within a single species may reflect adaptations to different environmental conditions, for example, taxa having the centrifugal arrangement are adapted to higher moisture conditions. Section REPENTIA (distal glumes and proximal lemmas with conspicuous nerves, proximal floret paleate) includes perennials of moist habitats (sea beaches, river banks, moist grasslands). *Panicum amarum* Ell., *P. repens* L., and *P. virgatum* L. are our representatives of this section. Typical NAD-me leaf anatomy, with chloroplasts disposed centripetally in the outer bundle sheath cells, is present in all species that have been examined.

Species of subg. AGROSTOIDES have a single bundle sheath around each major vascular bundle in the leaves; chloroplasts in the bundle sheath cells are arranged centrifugally. The decarboxylation pathway of these C_4 grasses is the NADP-me system (Ohsugi & Murata, 1986; Zuloaga, 1987a). The proximal glumes lack nerves or may have up to

three nerves, and the distal glume and proximal lemma each have three to five nerves. Chromosome numbers in subg. *Agrostoides* are based on either 9 or 10. Species of seven sections are present in the New World; two sections are represented in the Southeast. Section AGROSTOIDEA (Hitchc. & Chase) Hsu (spikelets long-ellipsoid, appressed to the inflorescence branches) includes *P. anceps* Michx., beaked panicum, and *P. rigidulum* Nees, both in wet habitats in the Southeast. Section TENERA (Hitchc. & Chase) Pilger (spikelets ellipsoid, congested on short pedicels) contains a single species in our area, *P. tenerum* Beyr. ex Trin. All other members of the section are Neotropical.

Subgenus PHANOPYRUM and subg. DICHANTHELIUM contain all of the species of *Panicum* utilizing the C_3 photosynthetic pathway, i.e., lacking kranz leaf anatomy (Brown & Smith; Zuloaga, 1987a). Their leaves have vascular bundles surrounded by two bundle sheaths, with both the inner mestome and outer parenchymatous sheaths consisting of thick-walled cells, and the cells of the outer sheath nearly or entirely devoid of chloroplasts. Inflorescences of species of subg. *Phanopyrum* vary from open, lax panicles to panicles with spikelets on racemose branches. Base chromosome numbers in subg. *Phanopyrum* are 9 and 10.

Subgenus PHANOPYRUM contains nine sections in the New World, with only two represented in the Southeast and elsewhere in North America. Hsu (1965) considered this subgenus to be the most primitive in the genus, and the stock from which all other *Panicum* lineages were derived. Section PHANOPYRUM Raf. (plants perennial with succulent stems, leaves usually several centimeters wide, spikelets lanceolate, appressed to the branches, proximal glumes almost as long as the spikelets, distal glumes and proximal lemmas not tuberculate, distal lemmas and paleas not pilose or rugose, florets separated by an elongated rachilla internode) contains *P. gymnocarpon* Ell., savannah panicum, which occurs from North Carolina southward on the Coastal Plain in our region, and also in the southern half of Arkansas. It is a large grass of wet forests. Section VERRUCOSA (Hitchc. & Chase) Hsu (plants annual with thin stems, leaves narrow, spikelets obovoid, on spreading pedicels, proximal glumes minute, distal glumes and proximal lemmas tuberculate ('warty'), distal lemmas and paleas pilose, longitudinally rugose, florets not separated by an elongated rachilla internode) contains only *P. verrucosum* Muhl., warty panicum, in our area. In the African species of *Panicum* sect. *Verruculosa* Stapf and in miscellaneous other species that appear to have 'warts' on the spikelet bracts the basal cell of some bicellular microhairs is enlarged and wart-like, and the distal cell is reduced (H. Scholz). However, the protuberances of *P. verrucosum* are not derived from modified hairs; they are formed from a group of elevated epidermal cells. Thus, the 'warts' of *P. verrucosum* are not homologous to 'warts' in other groups of *Panicum*.

Subgenus DICHANTHELIUM is the most familiar and most diverse taxonomic group of *Panicum* in North America. Its center of diversity is

in the Southeast. Twenty-six species are currently recognized in North America (Gould & Clark), of which eighteen occur in Florida (Hansen & Wunderlin), seventeen in Mississippi (Gould & Clark; Lelong, 1986), and fifteen in Arkansas (Gould & Clark; E. Smith). Species diversity declines northward, but in, for example, Michigan, fourteen species are known (Stephenson). The ranges of fifteen species extend into Mexico, where they generally occur at high elevations in pine and oak woodlands and in wet habitats (Gould, 1980), and a few of these species also occur in South America (Gould & Clark; Zuloaga, 1987a). Species distinctions are notoriously difficult in this subgenus, mainly because of the confounding influences of autogamy and hybridization, which have led to the formation of many variants and morphological intermediates that usually breed true. Fernald (1934, p. 62), himself notorious as a splitter of minor infraspecific taxa in numerous genera, commented on the profusion of species in this subgenus, "... *Panicum* suddenly became a favorite source of proposed new species, especially by younger men with little or no background of general scholarship and with a minimum of experience in exact and judicious consideration of other groups, whose specific evaluations were of a conveniently mechanical uniformity not consistent with the behavior of plants in Nature." He considered the treatment of Hitchcock & Chase (1910) to be on the right track (Fernald, 1921, 1934).

Subgenus *Dichanthelium* is relatively easy to recognize, at least as it is represented in the Temperate Zone of North America, because most of its species develop a rosette of short and broad basal leaves, exhibit two bursts of flowering activity with associated panicle dimorphism, and have ellipsoid to obovoid spikelets with rather small proximal glumes (usually less than $1/2$ the length of the spikelet). The distal palea has evenly distributed, simple papillae covering the outer surface. The terminal vernal panicles are characteristically open and consist of spreading branches, while the autumnal panicles are axillary and often more contracted because they are partially enclosed in overlapping leaf sheaths. Because of this suite of character states, *Dichanthelium* has been used at the rank of genus by some North American agrostologists (Brown & Smith; Clark & Gould; Gould, 1974; Gould & Clark). However, Pohl (1980), Zuloaga (1987a), and others have pointed out that all of these character states are represented, alone or in various combinations, in other subgenera, and that not all of them are present in all species of *Dichanthelium*. Thus, given the variation patterns exhibited by the genus in a worldwide context, *Dichanthelium* is best treated as a subgenus.

Hitchcock & Chase (1910) were the first authors to consider carefully the variation patterns within subgenus *Dichanthelium*. They chose to recognize informal species groups, sixteen of which contain species in the Southeast (Depauperata, Laxiflora, Angustifolia, Bicknelliana, Nudicaulia, Dichotoma, Spreta, Lanuginosa, Columbiana, Sphaerocarpa, Ensifolia, Lancearia, Oligosanthia, Scoparia, Commutata, and Latifolia). These groups all fall within sect. *DICHOTOMA* (Hitchc. &

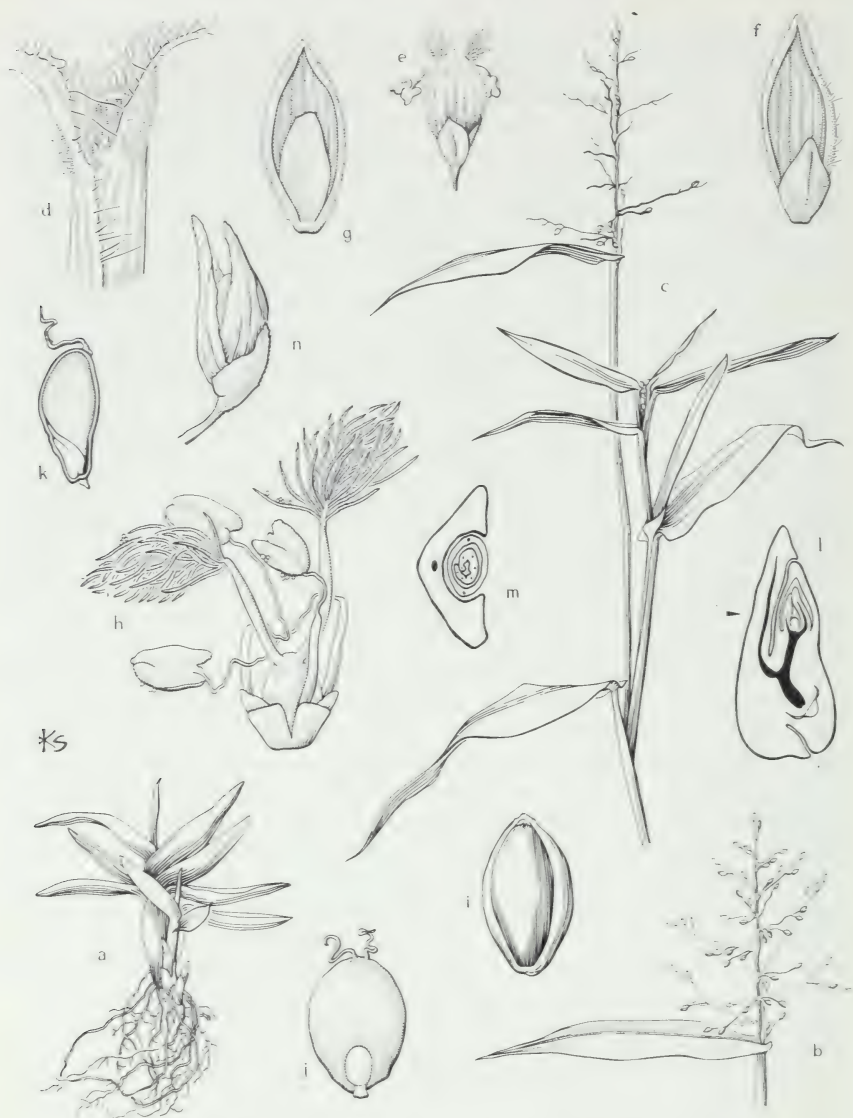


FIGURE 2. *Panicum*. a-m, *P. clandestinum* (subg. *DICHANTHELIUM*): a, part of winter rosette of leaves, $\times 1/2$; b, inflorescence of chasmogamous spikelets, $\times 1/2$; c, upper part of plant, chasmogamous spikelets in fruit or shed from inflorescence, inflorescence of cleistogamous spikelets below, $\times 1/2$; d, detail of upper part of leaf sheath, base of blade, and ligule, $\times 6$; e, chasmogamous spikelet at anthesis, pollen already shed from anthers, 1 stamen not visible, $\times 6$; f, small first and larger second glume, $\times 10$; g, sterile lemma (pubescent) and sterile palea, $\times 10$; h, flower of cleistogamous spikelet (note shriveled staminal filaments, pollen on stigmas, and lodicules), $\times 20$; i, fertile lemma (behind) and palea enclosing mature caryopsis, $\times 10$; j, mature

Chase) Hsu.⁹ The species groups are differentiated largely on the basis of vegetative features, including leaf blade shape and size, pubescence type and distribution, autumnal branching pattern, and ligule size, although spikelet size, shape, and pubescence are also used. Most of the species groups of subg. *Dichanthelium* were accorded sectional rank by Hsu (1965), but they have been merged into a single section by Zuloaga (1987a). The species occurring in our area are *P. aciculare* Desv. ex Poiret, *P. acuminatum* Sw., *P. boreale* Nash, *P. Boscii* Poiret, *P. clandestinum* L., *P. commutatum* Schultes, *P. consanguineum* Kunth, *P. depauperatum* Muhl., *P. dichotomum* L., *P. erectifolium* Nash, *P. latifolium* L., *P. laxiflorum* Lam., *P. linearifolium* Scribner, *P. malacophyllum* Nash, *P. oligosanthos* Schultes, *P. ovale* Ell., *P. Ravenelii* Scribner & Merr., *P. sabulorum* Lam., *P. scabriusculum* Ell., *P. scoparium* Lam., *P. sphaerocarpon* Ell., and *P. strigosum* Muhl.

The only other New World section included in subg. *Dichanthelium* by Zuloaga (1987a) is sect. *Cordovensia* (Hitchc. & Chase) Parodi, which differs from sect. *Dichotoma* in having larger proximal glumes and lacking a palea in the proximal florets. Section *Cordovensia* contains five species occurring in humid, shady places from Mexico to Argentina.

Gould & Clark have produced the most thorough modern revision of the North American taxa. Variability in a few species complexes (e.g., *P. aciculare*; Allred & Gould) has been clarified. A group of Hawaiian species has recently been transferred to subg. *Dichanthelium* (sect. *Turfosa* Pilger; Brown & Smith; Gould & Clark), which, if correct, is intriguing, because most of the Hawaiian flora has affinities with Australasia, not North America (the tarweeds (Asteraceae; Heliantheae; Madiinae) are a notable exception).

Subgenus *STEINCHISMA* has also been recognized as a distinct genus by some authors. The presence of evenly distributed compound papillae on the outer surface of the distal palea and expansion of the proximal palea with the onset of spikelet maturation are two character states cited by

caryopsis, adaxial surface (note shriveled styles and hilum), $\times 12$; k, diagrammatic longitudinal section of caryopsis, embryo to left, adaxial side to right, hilum to right of embryo, aleurone layers densely stippled, endosperm lightly stippled, $\times 12$; l, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing internode between scutellar and coleoptilar nodes, no epiblast, and cleft between base of scutellum and coleorhiza; m, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "l," showing numerous vascular bundles and overlapping margins of leaf. n, *P. anceps* (subg. AGROSTOIDES): spikelet in fruit, first glume to lower right, second glume to left, sterile lemma and tip of fertile lemma visible, $\times 10$. (Diagrammatic sections "l" and "m" after Reeder, 1957, fig. 12.)

⁹Zuloaga (1987a) calls this sect. *Dichanthelium*, but since subg. *Dichanthelium* does not include the type species of *Panicum*, the autonym does not automatically become the correct name for this taxon. Section *Dichotoma* (Hitchc. & Chase) Hsu, with *P. dichotomum* L. as its type species [and also the type species of subg. *Dichanthelium* (Hitchcock & Chase, 1910)] appears to be the earliest available name for this taxon.

Zuloaga (1987a) to distinguish it from other groups of *Panicum*. However, intermediate states are known in species of subg. *Phanopyrum* sect. *Laxa* (Hitchc. & Chase) Pilger and subg. *Steinchisma*, and artificial hybrids have been produced between members of these groups. The photosynthetic pathway in subg. *Steinchisma* is peculiar, being intermediate between the C_3 and C_4 pathways. The leaves have kranz anatomy, but there are fewer organelles than usual in the outer sheath. The base chromosome number is 10. *Panicum hians* Ell., gaping panicum, the type species of the subgenus, is our representative. It grows in open, wet habitats, such as marshes, ditches, and shores of lakes and ponds.

Panicum is one of very few grass genera that has an unequivocal fossil record, largely due to the efforts of Thomasson (1978, 1985, 1987). *Panicum elegans* Elias, from late Miocene–early Pliocene deposits in Kansas, has a well developed germination flap and irregularly arranged simple, rounded papillae on the distal lemma. The epidermal cell pattern of the distal floret and attachment scar of the distal lemma are also consistent with the features of *Panicum*, and more specifically, subg. *Dichanthelium*. Fossils of *Panicum* have also been found in the Miocene of New Mexico, Texas, Nebraska, and Colorado, and probable leaf impressions and/or distal floret impressions are known from the Miocene of Germany, Austria, Switzerland, and France. Thus, the genus has been in existence, much as we know it, for at least 5.5 million years.

Many species of *Panicum* have been examined cytologically (Bolhovskikh *et al.*). The great majority of the North American species are diploid ($2n = 18$), but several are tetraploid (e.g., *P. Boscii*, Gould, 1958; *P. clandestinum*, Moore *et al.*, Spellenberg, 1970a; *P. miliaceum* L., Parfitt & Harriman, Strid; *P. xanthophysum* Gray, Bowden, Löve & Löve), some are hexaploid (e.g., *P. dichotomiflorum*, Parodi), and a few exhibit multiple ploidy levels (e.g., *P. bulbosum* Kunth, Brown, 1951; *P. obtusum* Kunth, Brown, 1951; *P. virgatum*, Barnett & Carver, Burton, 1942, Löve & Löve, McMillan & Weiler, Moore *et al.*).

Panicum coloratum is variable cytologically. Pritchard & DeLacy found three morphotypes to be largely tetraploid ($2n = 36$), with occasional pentaploid and one heptaploid plants. One morphotype was diploid, and one was uniformly hexaploid (see also Jauhar & Joshi, 1968). Meiosis was regular in all of the euploid lines. In the pentaploid plants nine univalents were usually associated with the expected bivalents. Examination of meiotic pairing relationships in experimentally produced hybrids between the morphotypes showed that the tetraploids and hexaploids were allopolyploids, and that the hexaploid had two genomes in common with the tetraploid. All euploid types set seed following open pollination. The degree of self-incompatibility was variable both within and between morphotypes (Pritchard & DeLacy). Hutchison & Bashaw also found *P. coloratum* to reproduce sexually, but other members of the complex showed evidence of apomictic reproduction.

Hybrids among species of subg. *Dichanthelium* have been produced and analyzed by Spellenberg (1970b, 1975a, b). Certain hybrids, such as *P. ×shastense* Nash (*P. pacificum* Hitchc. & Chase × *P. occidentale* Scribner & Merr.), are completely sterile. There is no evidence of backcrossing in the field. At present, there appears to be no opportunity for gene flow between the parents. However, under experimental conditions where later generation (F_2 , F_3) hybrids were produced, levels of fertility increased, indicating the possibility that this mechanism could also give rise to new recombinants in the wild. Species complexes, for example that involving *P. acuminatum* (incl. *P. lanuginosum* Ell., *P. implicatum* Britton) exhibit varying degrees of genetic isolation. Spellenberg (1975b) recommended treating the most distinctive of these as varieties. In the *P. coloratum* complex (subg. *Panicum*), interspecific hybridization is prevented by arrested pollen tube growth in the gynoecium (Burson & Young).

Meiosis was regular in species of various ploidy levels (diploid to hexaploid) in the 'Laxa' group (Bouton *et al.*; these species actually belong to several different groups, including subg. *Phanopyrum* sect. *Laxa* (Hitchc. & Chase) Pilger, subg. *Agrostoides* sect. *Prionitia* Zuloaga, and subg. *Steinchisma*, as currently treated by Zuloaga, 1987a). All of these groups have a base chromosome number of 10. Only one tetraploid plant of *P. prionitis* Griseb. produced quadrivalents and double embryo sacs. All plants of the 'Laxa' group had high pollen fertility, and most of them showed high seed set when self-pollinated. The only exceptions were diploid *P. prionitis* and tetraploid *P. laxum* Sw., which had no seed set. This result could arise through either an incompatibility system or uncontrolled experimental conditions. Replication and additional evidence are needed to confirm the existence of an incompatibility system.

Panicum miliaceum is morphologically very variable but there is very little genetic variability at enzyme loci. Only two of eleven enzyme systems have detectable variation. Fixed heterozygosity in this species may extend the range of environments in which it can survive and may also account for the low degree of divergence between cultivated and weedy types (Warwick).

There is some evidence that certain species, or at least certain races within species, are out-breeders. In open pollination experiments with *P. coloratum*, phenotypic characters were found to segregate, especially within crosses of var. *makarikariense* (Lloyd & Thompson).

Species of subg. *Dichanthelium* have two distinct flowering periods during each growing season. Different reproductive syndromes are associated with each. Flowers of vernal inflorescences exhibit chasmogamy, while flowers of autumnal inflorescences are cleistogamous. Shinners (1944) noted that the pollen of vernal flowers is often highly sterile, while that of fall flowers is fertile. In New Jersey populations of *Panicum clandestinum*, viable seed production by cleistogamous flowers is ten times that by chasmogamous flowers. Other features of reproductive biology, including rate of germination, were also higher

in cleistogamous flowers. In fact, under all conditions chasmogamous reproductive effort is less than cleistogamous reproductive effort in this species (Bell & Quinn, 1987). However, seeds that achieve maturity in both types of flowers have equal fitness under most conditions. The reproductive strategies exhibited by plants of subg. *Dichanthelium* lead to flexible and diverse potentials for persistence and dispersal. Offspring from cleistogamous flowers have genotypes presumably identical to those of the parent plants. These seeds are not dispersed over great distances, and they germinate rapidly. On the other hand, seeds from chasmogamous flowers have a longer period of dormancy, and may be more important for dispersal over time (Bell & Quinn, 1985).

Most species of *Panicum* lack specialized structures to facilitate dispersal of propagules. A few species have dehiscent 'tumbleweed' inflorescences (e.g., *P. capillare*, *P. hippothrix* K. Schum.). Others have thickened rachilla internodes that may serve as elaiosomes (e.g., *P. cervicatum* Chase, *P. Trinii* Kunth, *P. vinaceum* Swallen) (Davidse, 1987). However, most species of *Panicum* appear to disperse seeds locally in a rather passive manner.

Some attention has been focused on interactions between *Panicum* species and other organisms with which they grow. East African populations of *P. coloratum* under heavy grazing are more frequently associated with mycorrhizal fungi. The mycorrhizal fungi also promote prostrate shoot formation and enhanced root growth, both of which increase survivability under grazing pressure (Wallace). Dead leaf and stem biomass of *P. virgatum* is colonized by various fungi that presumably recycle nutrients in the prairie and dune ecosystems in which it occurs (Gabel & Tiffany, 1987a, b; Helin). *Panicum trypheron* Schultes serves as a reservoir for the false smut of rice (*Ustilaginoidea virens* (Cke.) Tak.) when rice is not available for infection (Shetty & Shetty). Several species of *Panicum* serve as hosts for two strains of maize dwarf mosaic virus and sugarcane mosaic virus (Rosenkranz). *Panicum* mosaic virus, which causes stunting, chlorosis, and necrosis, and leads to reductions in seed and forage production, was characterized from *P. virgatum*, but it is also capable of infecting other panicoids (Sill & Pickett).

Panicum amarulum Hitchc. & Chase (= *P. amarum* var. *amarulum* (Hitchc. & Chase) Palmer; Palmer), bitter panicum, is an important native dune grass of the southeastern Coastal Plain. It is relatively salt tolerant. Its seeds require a cold treatment of 15 days or more to ensure good germination (Seneca, 1969). Following germination, seedling growth is also affected by salinity levels. Seedlings growing without NaCl were unhealthy and showed symptoms of mineral deficiency. At levels below 2 percent NaCl, no evidence of salt stress appeared. Although growth was affected in seedlings growing at 2 percent NaCl, this species was able to grow better at this level of salt than other associated dune grasses such as *Ammophila breviligulata* Fern., American beachgrass, and *Uniola paniculata* L., sea oats (Seneca, 1972). *Panicum amarulum* has been used in experiments on the stabilization of

foredunes and inland sandy areas. It can stabilize sandy areas, even when a substantial amount of sand movement occurs. New shoots are capable of growing after being buried by up to 15 cm of sand. However, it appears to be less efficient at trapping sand than *A. breviligulata* or *U. paniculata*. *Panicum amarulum* also has a shorter growing season (May–October) than *A. breviligulata*, and more widely spaced leaves, both of which may also contribute to less efficient sand-trapping ability (Seneca *et al.*).

Panicum hemitomon is a major component of lake shore and marsh communities. It rapidly colonizes areas that have been cleared (by fire, for example), and forms dense colonies that may then exclude or inhibit the establishment of competitors (Lowe). However, it is intolerant of eutrophication (H. Brown) and salination (Pezeshki *et al.*, 1987a, b) and may thus serve as a useful indicator of environmental quality or change.

Panicum virgatum is also an important sand-binder of dunes and prairies. It prefers wet mesic, sandy loam prairies in the Midwest (Abrams & Hulbert; Faber-Langendoen & Maycock). Its seeds exhibit innate dormancy in the autumn. Zhang & Maun found that dormancy could be broken by storage in moist cool conditions. Exposure of moist seeds to relatively high temperatures also broke dormancy. Neither dry storage nor light had a significant effect in breaking dormancy.

Panicum hians (incl. *P. milioides* Nees ex Trin.; Zuloaga, 1987a), with its intermediate C_3/C_4 leaf anatomy and physiology (Brown & Brown; Kanai & Kashiwagi), has been the subject of much observation and experimentation. Ku & Edwards speculated that it might be more efficient than C_3 species in utilizing low levels of CO_2 at given atmospheric oxygen concentrations. However, it has been shown to have only 15–30 percent of the photosynthetic activity of C_4 species under uniform conditions (Rathnam & Chollet, 1978, 1979a, b). It is more similar in physiology to C_3 species, and there is no direct relationship between a low CO_2 compensation point, high temperature environment, and superior growth. Thus, there is no clear reason why an intermediate photosynthetic-photorespiratory pathway has evolved (Fladung & Hesselbach).

Because of the range of chlorenchyma types found in *Panicum*, attempts have also been made to assess ontogenetic origins of the cell types. The origin and development of bundle-sheath and mesophyll cells have been compared (Dengler *et al.*) in *P. effusum* R. Br. (NAD-me type) and *P. bulbosum* Kunth (NADP-me type). In *P. effusum* both mesophyll and chlorenchymatous bundle-sheath cells are derived from the ground meristem, whereas in *P. bulbosum* the bundle-sheath cells arise from the procambium and the mesophyll cells from the ground meristem. The earlier developmental divergence of chlorenchymatous bundle-sheath cells and mesophyll cells in the latter may provide the additional time needed to account for other associated structural differences in leaf anatomy of these two types.

A correlation has been found between the presence or absence of a suberized lamella and the location of chloroplasts within the bundle sheath cells (Ohsugi *et al.*, 1988). In species with centrifugally positioned chloroplasts, a suberized lamella is present, but it is absent when the chloroplasts are centripetally arranged. There also appears to be a difference in the site of activity of the enzyme sucrose phosphate synthase. When chloroplasts are centrifugally arranged, sucrose biosynthesis occurs in the mesophyll cells, but it occurs in the bundle sheath cells when centripetally arranged chloroplasts are present (Ohsugi *et al.*, 1988). There is, however, contrary evidence with regard to the question of the presence or absence of a suberized lamella. On the basis of their histochemical, anatomical, and physiological studies, Eastman *et al.* (1988a, b) call into question whether or not any grasses have suberized lamellae.

Many of the annual species of *Panicum* are considered to be weeds. In our region most of these are relatively innocuous plants of waste areas and roadsides. However, a few can become serious weeds of cultivated crops such as corn (*Zea Mays* L.). *Panicum miliaceum* contains a number of weedy and cultivated forms. Cavers and his colleagues and students (Bough *et al.*; McCanny *et al.*, 1988a, b; Moore & Cavers) have characterized many of the biotypes that behave as weeds in Canada and the northern United States and have monitored their spread. Farm equipment serves as one means of dispersal, although the effectiveness of this mechanism varies among biotypes. A black-seeded biotype is much more efficiently dispersed in this way than is a golden-seeded one (McCanny & Cavers, 1988).

Species that appear as occasional weeds in Britain include *Panicum capillare*, *P. dichotomiflorum*, *P. effusum*, *P. laevifolium* Hackel, and *P. miliaceum* (Hanson & Mason). *Panicum dichotomiflorum* has recently become invasive in Yugoslavia (Ilijanic & Markovic). Some perennials are also aggressive weeds. For example, *P. repens* spreads by rhizomes that are tolerant of desiccation. It grows well in a range of soil conditions but cannot withstand cold (Wilcut *et al.*, 1988a, b). It can reduce the yield or cover of *Cynodon dactylon* (L.) Pers., an important lawn grass in the Southeast.

Many perennial species are important forage crops in tropical and subtropical regions, and several are important sand-binders in arid areas. Across the area from North Africa to India, *P. turgidum* Forskål serves as both a sand-binder and a forage grass. It is extremely drought resistant and is grazed even in its dry state by camels and donkeys. Its straw is used for weaving and thatching. The powder from its ground stems is used for treating wounds in the central Sahara Desert (Williams & Farias). Many species are important forage grasses in less harsh environments (Hutchison & Bashaw; Nielsen, 1944; Ochi & Nakajima; Roshevits). In a survey of the digestibility of plants of 28 species of *Panicum*, those of species with non-kranz anatomy and C₃ photosynthesis were more digestible and had less cell-wall content than C₃/C₄ intermediates, which in turn were more digestible than

C₄ species (Wilson *et al.*). Thus, members of subg. *Phanopyrum* and subg. *Dichanthelium* are more digestible than plants belonging to other subgenera.

Panicum coloratum var. *makarikariense* is also a highly palatable plant and is persistent on clay soils under conditions of waterlogging, drought, and heavy grazing. It has been introduced into tropical and subtropical areas of the world, including Australia, the southern United States, and Japan (Lloyd; Ochi & Nakajima). *Panicum sumatrense* Roth ex Roemer & Schultes contains a cultivated form (subsp. *sumatrense*; Indian millet, sama) that is used as a cereal grain in Asia (De Wet *et al.*, 1983).

Several species of *Panicum* have been used in traditional medicine. *Panicum turgidum* and *P. glutinosum* Vahl have been mentioned in this regard (Morton; Williams & Farias), and *P. antidotale* Retz., *P. miliaceum*, *P. sarmentosum* Roxb., and *P. sumatrense* were noted by Majumdar, although no specific ailments were given.

REFERENCES:

- Under references for tribe see BENTHAM; BLAKE; BLUMQUIST; BOLKHOVSKIKH *et al.*; BROWN (1951); BURTON (1942); BUTZIN (1970); CHASE (1911); CHIPPINDALL; CLARK & GOULD; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); EASTMAN *et al.* (1988a, b); GOULD (1958, 1975); HACKEL; HANSON & MASON; HITCHCOCK & CHASE (1910, 1951); HSU (1965); HUGHES; JONES & COILE; KOYAMA; LÖVE & LÖVE; MACROBERTS; MCNEILL & DORE; NASH (1903); PARFITT & HARRIMAN; PARODI; POHL (1947, 1980); RADFORD *et al.*; ROSENKRANZ; ROSHEVITS; SHINNERS (1944, 1954); SILVEUS; E. SMITH; TSVELEV (1976); VOSS; WATSON & DALLWITZ; WEBSTER (1987, 1988); WUNDERLIN; and ZULOAGA & SÖDERSTROM.
- ABRAMS, M. D., & L. C. HULBERT. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *Am. Midl. Nat.* **117**: 442–445. 1987. [*P. virgatum* achieves the greatest cover on lowland soils in Kansas prairies.]
- ALLRED, K. W., & F. W. GOULD. Geographic variation in the *Dichanthelium aciculare* complex (Poaceae). *Brittonia* **30**: 497–504. 1978. [Numerical taxonomy, incl. principal components analysis.]
- ASHE, W. W. The dichotomous group of *Panicum* in the eastern United States. *Jour. Elisha Mitchell Sci. Soc.* **15**: 22–62. 1898. [Early uncritical monograph of subg. *Dichanthelium*.]
- . Some dichotomous species of *Panicum*. *Jour. Elisha Mitchell Sci. Soc.* **16**: 84–91. 1899. [Subg. *Dichanthelium*.]
- BARNETT, F. L., & R. F. CARVER. Meiosis and pollen stainability in switchgrass, *Panicum virgatum* L. *Crop Sci. Madison* **7**: 301–304. 1967. [Genetically based distinctions between upland and lowland morphotypes.]
- BASKIN, J. M., & C. C. BASKIN. Seasonal changes in the germination responses of fall panicum to temperature and light. *Canad. Jour. Pl. Sci.* **63**: 973–979. 1983. [*P. dichotomiflorum* has a period of innate dormancy in the fall, regardless of environmental conditions.]
- & ———. Seasonal changes in the germination responses of buried witchgrass (*Panicum capillare*) seeds. *Weed Sci.* **34**: 22–24. 1986. [Innate dormancy in the fall.]
- BAUM, B. R. Kalm's specimens of North American grasses—their evaluation for typification. *Canad. Jour. Bot.* **45**: 1845–1852. 1967. [Excludes Kalm's specimens in the lectotypification of *P. latifolium* L.; see VOSS (1972).]

- BELL, T. J., & J. A. QUINN. Relative importance of chasmogamously and cleistogamously derived seeds of *Dichanthelium clandestinum* (L.) Gould. Bot. Gaz. 146: 252-258. 1985.
- & ———. Effects of soil moisture and light intensity on the chasmogamous and cleistogamous components of reproductive effort of *Dichanthelium clandestinum* populations. Canad. Jour. Bot. 65: 2243-2249. 1987.
- BERG, R. Y. Spikelet structure in *Panicum australiense* (Poaceae): taxonomic and ecological implications. Austral. Jour. Bot. 33: 579-583. 1985. [= *Yakirra australiensis* (Domin) Lazarides & R. Webster.]
- BOUGH, M., J. C. COLOSI, & P. B. CAVERS. The major weedy biotypes of proso millet (*Panicum miliaceum*) in Canada. Canad. Jour. Bot. 64: 1188-1198. 1986.
- BOUTON, J. H., R. H. BROWN, J. K. BOLTON, & R. P. CAMPAGNOLI. Photosynthesis of grass species differing in carbon dioxide fixation pathways. VII. Chromosome numbers, metaphase I chromosome behavior, and mode of reproduction of photosynthetically distinct *Panicum* species. Pl. Physiol. 67: 433-437. 1981.
- BOWDEN, W. M. Chromosome numbers and taxonomic notes on northern grasses. III. Twenty-five genera. Canad. Jour. Bot. 38: 541-557. 1960. [*P. xanthophysum* Gray, $2n = 36$.]
- BROWN, H. D. Aquatic macrophytes of Lake Mize, Florida, 1968-1980. Bull. Torrey Bot. Club 114: 180-182. 1987. [Population of *P. hemitomom* increased greatly upon eutrophication of the lake and declined to pre-enrichment levels as water quality improved.]
- BROWN, R. H. Photosynthesis of grass species differing in carbon dioxide fixation pathways. IV. Analysis of reduced oxygen response in *Panicum milioides* and *Panicum Schenckii*. Pl. Physiol. 65: 346-349. 1980.
- , J. H. BOUTON, P. T. EVANS, H. E. MALTER, & L. L. RIGSBY. Photosynthesis, morphology, leaf anatomy, and cytogenetics of hybrids between C_3 and C_3/C_4 *Panicum* species. Pl. Physiol. 77: 653-658. 1985. [Intermediate anatomical and physiological features in hybrids.]
- , L. RIGSBY, & M. RIGLER. Photosynthesis of grass species differing in carbon dioxide fixation pathways. VIII. Ultrastructural characteristics of *Panicum* species in the *laxa* group. Pl. Physiol. 71: 425-431. 1983.
- & W. V. BROWN. Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. Crop Sci. Madison 15: 681-685. 1975. [First characterization of the intermediate physiology and anatomy of this species (= *P. hians*).]
- BROWN, W. V. *Panicum bennettense*, a new species from North Carolina. Bull. Torrey Bot. Club 69: 539-540. 1942.
- & B. N. SMITH. The genus *Dichanthelium* (Gramineae). Bull. Torrey Bot. Club 102: 10-13. 1975. [Outline of the characters of this group and reasons for treating it as a genus distinct from *Panicum*.]
- BURSON, B. L., & B. A. YOUNG. Pollen-pistil interactions and interspecific-incompatibility among *Panicum antidotale*, *P. coloratum*, and *P. deustum*. Euphytica 32: 397-405. 1983. [Cross-incompatible, with pollen tube inhibition occurring on the stigma or elsewhere in the pistil and micropyle never penetrated.]
- CARPENTER, J. L., & H. J. HOPEN. A comparison of the biology of wild and cultivated proso millet (*Panicum miliaceum*). Weed Sci. 33: 795-799. 1985. [Faster germination response in cultivated proso millet than in wild forms.]
- COLOSI, J. C., P. B. CAVERS, & M. A. BOUGH. Dormancy and survival in buried seeds of proso millet (*Panicum miliaceum*). Canad. Jour. Bot. 66: 161-168. 1988. [Crop and crop-like weed biotypes produce only transient seed banks, but black-seeded weed type survived for four years.]

- DENGLER, N. G., R. E. DENGLER, & P. W. HATTERSLEY. Comparative bundle sheath and mesophyll differentiation in the leaves of the C₄ grasses *Panicum effusum* and *P. bulbosum*. *Am. Jour. Bot.* **73**: 1431-1442. 1986.
- DE RUITER, J. M., J. C. BURNS, W. F. MCCLURE, & D. H. TIMOTHY. Prediction of cell wall carbohydrates and quality in *Panicum* species by near infrared reflectance spectroscopy. *Crop. Sci. Madison* **28**: 348-353. 1988. [Methodology paper; *P. amarum* vars. *amarum* and *amarulum*, *P. virgatum* examined.]
- DE WET, J. M. J., K. E. P. RAO, & D. E. BRINK. Systematics and domestication of *Panicum sumatrense* (Gramineae). *Jour. Agr. Trad. Bot. Appl.* **30**: 159-168. 1983. [Two cultivated races, but these cross readily and are not recognized formally.]
- DOWNTON, J., J. BERRY, & E. B. TREGUNNA. Photosynthesis: temperate and tropical characteristics within a single grass genus. *Science* **163**: 78, 79. 1969. [Early discussion of the distribution of kranz syndrome within *Panicum*.]
- EBERHART, S. A., & L. C. NEWELL. Variation in domestic collections of switchgrass, *Panicum virgatum* L. *Agron. Jour.* **51**: 613-616. 1959.
- EDWARDS, G. E., M. S. B. KU, & M. D. HATCH. Photosynthesis in *Panicum milioides*, a species with reduced photorespiration. *Pl. Cell Physiol.* **23**: 1185-1195. 1982. [= *P. hians* Ell.]
- FABER-LANGENDOEN, D., & P. F. MAYCOCK. Composition and soil-environment analysis of prairies on Walpole Island, southwestern Ontario. *Canad. Jour. Bot.* **65**: 2410-2419. 1987. [*Panicum virgatum* grows optimally in wet mesic, sandy loam sites in these long-grass prairies.]
- FAIRBROTHERS, D. E. Relationships in the *Capillaria* group of *Panicum* in Arizona and New Mexico. *Am. Jour. Bot.* **40**: 708-714. 1953. [Incl. hybrid index for population samples.]
- FERNALD, M. L. The Gray Herbarium expedition to Nova Scotia, 1920. *Rhodora* **23**: 223-245. 1921. [Discussion of species concepts and variability in selected taxa of *Panicum* subg. *Dichantherium*.]
- . Realignments in the genus *Panicum*. *Ibid.* **36**: 61-87. 1934. (Also publ. as *Contr. Gray Herb.* **103**.) [Keys, new combinations.]
- FLADUNG, M., & J. HESSELBACH. Effect of varying environments on photosynthetic parameters of C₃, C₃-C₄ and C₄ species of *Panicum*. *Oecologia* **79**: 168-173. 1989.
- FRECKMANN, R. W. New combinations in *Dichantherium* (Poaceae). *Phytologia* **39**: 268-272. 1978. [Limited discussion.]
- . The correct name for *Dichantherium leucoblepharis* (Poaceae) and its varieties. *Brittonia* **33**: 457, 458. 1981. [= *D. strigosum* (Muhl.) Freckmann.]
- GABEL, A. W., & L. H. TIFFANY. Life history of *Elsinoë panici*. *Proc. Iowa Acad. Sci.* **94**: 121-127. 1987a. [Widespread fungus on *P. virgatum* leaf and stem litter in Iowa.]
- & ———. Host-parasite relations and development of *Elsinoë panici*. *Myecologia* **79**: 737-744. 1987b.
- GARMAN, H. R., & L. V. BARTON. Germination of seeds of *Panicum anceps* Michx. *Contr. Boyce Thompson Inst.* **14**: 117-122. 1946.
- GOULD, F. W. Nomenclatural changes in the Poaceae. *Brittonia* **26**: 59, 60. 1974. [Elevates *Dichantherium* to generic rank; many new combinations in *Dichantherium*.]
- . The Mexican species of *Dichantherium* (Poaceae). *Ibid.* **32**: 353-364. 1980. [Key, descriptions.]
- & C. A. CLARK. *Dichantherium* (Poaceae) in the United States and Canada. *Ann. Missouri Bot. Gard.* **65**: 1088-1132. 1978. [Best available monograph for *Panicum* subg. *Dichantherium*.]
- HANSEN, B. F., & R. P. WUNDERLIN. Synopsis of *Dichantherium* (Poaceae) in Florida. *Ann. Missouri Bot. Gard.* **75**: 1637-1657. 1988. [Good regional treatment.]

- HELIN, J. A. Fungus flora of *Panicum virgatum* L. Proc. Iowa Acad. Sci. **68**: 139–143. 1961.
- HITCHCOCK, A. S. Notes on North American grasses. V. Some Trinius *Panicum* types. Bot. Gaz. **41**: 64–67. 1906.
- . Type of the genus *Panicum*. Rhodora **13**: 173–176. 1911. [Disputes Nieuwland's claims and notes errors in Nieuwland's paper (1911).]
- & A. CHASE. The North American species of *Panicum*. Contr. U.S. Natl. Herb. **15**: 1–396. 1910.
- HOLM, T. Some American *Panicums* in the Herbarium Berolinense and in the herbarium of Willdenow. U.S. Dep. Agr. Div. Agrost. Bull. **4**: 17–23. 1897.
- HUTCHISON, D. J., & E. C. BASHAW. Cytology and reproduction of *Panicum coloratum* and related species. Crop Sci. Madison **4**: 151–153. 1964. [*P. coloratum* L. and *P. Stapfianum* Fourcade reproduce sexually; *P. deustum* and *P. laevifolium* reproduce through sexual and apomictic means.]
- ILIJANIC, L., & L. MARKOVIC. *Panicum dichotomiflorum* Michaux in the surroundings of Zagreb. Acta Bot. Croat. **45**: 137–139. 1986. [A new adventive in the Yugoslavian flora.]
- IL'IN, V. A., Y. Y. KOZHEMYAKINA, & V. A. KRUPNOV. Genetic control of the grain color of millet, *Panicum miliaceum* L. Soviet Genet. **14**: 1494–1500. 1978. [At least four genes control grain color.]
- JAUHAR, P. P. Morphological studies in some species of *Panicum* L. Bull. Bot. Surv. India **8**: 183–188. 1966.
- . Studies on epidermal pattern in some species of *Panicum*. Jour. Indian Bot. Soc. **46**: 215–221. 1967.
- & A. B. JOSHI. Cytological studies in some species of *Panicum*. Cytologia **31**: 153–159. 1966.
- & ———. Accessory chromosomes in a new hexaploid species of *Panicum*. Caryologia **21**: 105–110. 1968. [A hexaploid form of *P. coloratum*.]
- KANAI, R., & M. KASHIWAGI. *Panicum milioides*, a Gramineae plant having kranz leaf anatomy without C₄-photosynthesis. Pl. Cell Physiol. **16**: 669–679. 1975. [= *P. hians* Ell.]
- KESSLER, J. W., & S. L. HATCH. In: IOPB chromosome number reports. LXXXII. Taxon **33**: 126–134. 1984. [*P. gymnocarpon*, 2n = 40.]
- KU, S. B., & G. E. EDWARDS. Photosynthetic efficiency of *Panicum hians* and *Panicum milioides* in relation to C₃ and C₄ plants. Plant Cell Physiol. **19**: 665–675. 1978. [These species now considered to be synonymous.]
- , & D. SMITH. Photosynthesis and nonstructural carbohydrate concentration in leaf blades of *Panicum virgatum* as affected by night temperature. Canad. Jour. Bot. **56**: 63–68. 1978.
- LAMSON-Scribner, F., & E. D. MERRILL. The New England species of the genus *Panicum*. Rhodora **3**: 93–129. 1901. [Key and new combinations.]
- LAŃCUCKA-ŚRODONIOWA, M. Tortonian flora from the "Gdów Bay" in the south of Poland. Acta Palaeobot. **7**: 1–133. pls. 1–7. 1966. [An Upper Miocene fruit, formerly attributed to *Panicum*, reidentified as *Ruppia*.]
- LAZARIDES, M. The Australian species referred to *Ichnananthus* Beauv. (Gramineae). Austral. Jour. Bot. **7**: 328–346. 1959. [Most transferred to *Panicum*.]
- . New taxa of tropical Australian grasses (Poaceae). Nuytsia **5**: 273–303. 1984. [*Arthragrostis* described to accomodate *Panicum deschampsoides* Domin.]
- & R. D. WEBSTER. *Yakirra* (Paniceae, Poaceae), a new genus for Australia. Brunonia **7**: 289–296. 1984.
- LELONG, M. G. New combinations for *Panicum* subgenus *Panicum* and subgenus *Dichantherium* (Poaceae) of the southeastern United States. Brittonia **36**: 262–273. 1984. [Lists of synonymy, keys and/or discussions of varieties in *P. rigidulum* Bosc ex Nees, *P. strigosum*, *P. dichotomum*, *P. ensifolium* Baldwin,

- P. chamaelonche* Trin., *P. portoricense* Desv. ex Hamilton, *P. acuminatum*, *P. ovale*.]
- . A taxonomic treatment of the genus *Panicum* (Poaceae) in Mississippi. *Phytologia* **61**: 251–269. 1986. [Good regional treatment.]
- LINDER, D. H. Some varieties of *Panicum virgatum*. *Rhodora* **24**: 11–16. 1922.
- LLOYD, D. L. Makarikari grass—(*Panicum coloratum* var. *makarikariense*)—a review with particular reference to Australia. *Trop. Grasslands* **15**: 44–52. 1981. [Agronomy.]
- & J. P. THOMPSON. Numerical analysis of taxonomic and parent-progeny relationships among Australian selections of *Panicum coloratum*. *Queensl. Jour. Agr. Anim. Sci.* **35**: 35–46. 1978.
- LOWE, E. F. The relationship between hydrology and vegetational pattern within the floodplain marsh of a subtropical Florida lake. *Florida Scientist* **49**: 213–233. 1986. [*P. hemitomon* colonizes burned marshes.]
- MAJUMDAR, R. B. The genus *Panicum* Linn. in India. *Bull. Bot. Soc. Bengal* **27**: 39–54. 1973. [Key, descriptions, spikelet illustrations.]
- MATTHEI, O. Las especies del género *Panicum* L. (Poaceae) en Chile. *Gayana Bot.* **44**: 25–32. 1987. [Two naturalized, weedy species and two native species of sandy shores and dunes; *Dichanthelium* and other segregates not included.]
- MCCANNY, S. J., M. BOUGH, & P. B. CAVERS. Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. I. Rate of spread and crop susceptibility. *Weed Res.* **28**: 59–65. 1988.
- & P. B. CAVERS. The escape hypothesis: a test involving a temperate, annual grass. *Oikos* **49**: 67–76. 1987. [Greater survivability of seeds dispersed farther away from parent source supports hypothesis.]
- & ———. Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. *Weed Res.* **28**: 67–72. 1988.
- McMILLAN, C., & J. WEILER. Cytogeography of *Panicum virgatum* in central North America. *Am. Jour. Bot.* **46**: 590–593. 1959. [Chromosome number in populations.]
- MERRILL, E. D. A criticism on certain new species of *Panicum*. *Bull. Torrey Bot. Club* **27**: 593–597. 1900. [Critical of Ashe's monographs, both in terms of species concepts and carelessness with nomenclature.]
- MOORE, D. R. J., & P. B. CAVERS. A comparison of seedling vigour in crop and weed biotypes of proso millet (*Panicum miliaceum*). *Canad. Jour. Bot.* **63**: 1659–1663. 1985. [Black-seeded weed biotype has many of the characteristics predicted for a wild form of a crop.]
- MOORE, R. J., W. G. DORE, & J. MCNEILL. In: IOPB chromosome number reports. LIII. *Taxon* **25**: 483–500. 1976. [*P. latifolium* var. *clandestinum* (L.) Pursh (= *P. clandestinum*), $2n = 36$; *P. virgatum*, $2n = 72$.]
- MORGAN, J. A., R. H. BROWN, & B. J. REGER. Photosynthesis in grass species differing in carbon dioxide fixation pathways. III. Oxygen response and enzyme activities of species in the *Lara* group of *Panicum*. *Pl. Physiol.* **65**: 156–159. 1980.
- NARAYANASWAMI, S. The structure and development of the caryopsis in some Indian millets. III. *Panicum miliare* Lamk. and *P. miliaceum* Linn. *Lloydia* **18**: 61–73. 1955.
- NEWMAN, P. R., & L. E. MOSER. Seedling root development and morphology of cool-season and warm-season forage grasses. *Crop Sci. Madison* **28**: 148–151. 1988. [Roots from subcoleoptile internode ubiquitous, adventitious roots common in *P. virgatum*.]
- NIELSEN, E. L. Analysis of variation in *Panicum virgatum*. *Jour. Agr. Res.* **69**: 327–353. 1944.
- . Polyploidy and winter survival in *Panicum virgatum* L. *Jour. Am. Soc. Agron.* **39**: 822–827. 1947. [No relationship.]

- NIEUWLAND, J. A. The type of the genus *Panicum*. *Am. Midl. Nat.* **2**: 60–65. 1911.
[Type designated as *P. italicum* L. (= *Setaria viridis* subsp. *italica* (L.) Briq.); *Chasea* described to replace *Panicum*, and new combinations made.]
- OCHI, M., & K. NAKAJIMA. Characteristics and classification of species and strains of *Panicum*. I. Agronomic characteristics and classification of *Panicum* accessions introduced to Japan. (In Japanese.) *Bull. Natl. Grassland Res. Inst. Japan* **11**: 78, 79. 1977.
- OHNISHI, J.-I., & R. KANAI. Pyruvate uptake by mesophyll and bundle sheath chloroplasts of a C₄ plant, *Panicum miliaceum* L. *Plant Cell Physiol.* **28**: 1–10. 1987.
- & ———. Light-dependent uptake of pyruvate by mesophyll chloroplasts of a C₄ plant, *Panicum miliaceum* L. *Ibid.* 243–251. 1987.
- OHSUGI, R., & S. C. HUBER. Light modulation and localization of sucrose phosphate synthase activity between mesophyll cells and bundle sheath cells in C₄ species. *Pl. Physiol.* **84**: 1096–1101. 1987.
- & T. MURATA. Leaf anatomy, post-illumination CO₂ burst and NAD-malic enzyme activity of *Panicum dichotomiflorum*. *Pl. Cell Physiol.* **21**: 1329–1333. 1980.
- & ———. Variations in the leaf anatomy among some C₄ *Panicum* species. *Ann. Bot. II.* **58**: 443–453. 1986. [Subtypes within some NAD-me species.]
- , ——— & N. CHONAN. C₄ syndrome of the species in the *Dichotomiflora* group of the genus *Panicum* (Gramineae). *Bot. Mag. Tokyo* **95**: 339–347. 1982.
- , M. SAMEJIMA, N. CHONAN, & T. MURATA. $\delta^{13}\text{C}$ values and the occurrence of suberized lamellae in some *Panicum* species. *Ann. Bot. II.* **62**: 53–59. 1988.
- PALACIOS, R. A. Variaciones en la estructura de las espiguillas en algunas especies argentinas de *Panicum*. *Bol. Soc. Argent. Bot.* **12**: 38–43. 1968. [Spikelet structure illustrated.]
- PALMER, P. G. A biosystematic study of the *Panicum amarum*-*P. amarulum* complex (Gramineae). *Brittonia* **27**: 142–150. 1975. [*P. amarulum* a variety of *P. amarum*.]
- PATRICK, T. S., B. E. WOFFORD, & D. H. WEBB. State records and other recent noteworthy collections of Tennessee plants. IV. *Castanea* **48**: 109–116. 1983. [*P. hemitomon*, Grundy Co.]
- PEZESHKI, S. R., R. D. DELAUNE, & W. H. PATRICK. Response of the freshwater marsh species, *Panicum hemitomon* Schult., to increased salinity. *Freshwater Biol.* **17**: 195–200. 1987a.
- , ——— & ———. Gas exchange characteristics of Gulf of Mexico coastal marsh macrophytes. *Jour. Exper. Mar. Biol. Ecol.* **111**: 243–253. 1987b. [Less efficient water use during photosynthesis in *P. hemitomon* than in species of *Spartina*.]
- PIZZOLATO, T. D. A three-dimensional reconstruction of the vascular system to the lodicules, androecium, and gynoecium of a fertile floret of *Panicum dichotomiflorum* (Gramineae). *Am. Jour. Bot.* **70**: 1173–1187. 1983. [No xylem discontinuity in the floret steles of *Panicum* or *Echinochloa*, in contrast to *Oryza* L.]
- PRITCHARD, A. J., & I. H. DELACY. The cytology, breeding system and flowering behaviour of *Panicum coloratum*. *Austral. Jour. Bot.* **22**: 57–66. 1974.
- RATHNAM, C. K. M., & R. CHOLLET. CO₂ donation by malate and aspartate reduces photorespiration in *Panicum milioides*, a C₃-C₄ intermediate species. *Biochem. Biophys. Res. Commun.* **85**: 801–808. 1978. [= *P. hians*.]
- & ———. Phosphoenolpyruvate carboxylase reduces photorespiration in *Panicum milioides*, a C₃-C₄ intermediate species. *Arch. Biochem. Biophys.* **193**: 346–354. 1979a. [= *P. hians*.]

- & ———. Photosynthetic carbon metabolism in *Panicum milioides*, a C₃-C₄ intermediate species: evidence for a limited C₄ dicarboxylic acid pathway of photosynthesis. *Biochim. Biophys. Acta* **548**: 500-519. 1979b. [= *P. hians*.]
- RENOUZE, S. A. The genus *Panicum* group *Lorea* (Gramineae). *Kew Bull.* **32**: 419-428. 1978. [High altitude Neotropical group.]
- . A new species of *Acroceras* (Gramineae) from tropical Africa. *Ibid.* **34**: 556. 1980. [Similarities between *Acroceras* and *Panicum*.]
- REYES, C. R. Gramineas del Estado Portuguesa. El género *Panicum*. *Biolllania* **4**: 29-59. 1985. [Twenty-six species in this Venezuelan state; inclusive generic concept (incl. *Dichantherium*, part of *Urochloa*).]
- ROTHWELL, N. V. Evidence for diverse cell types in the apical region of the root epidermis of *Panicum virgatum*. *Am. Jour. Bot.* **53**: 7-11. 1966.
- ST. JOHN, H. Diagnoses of *Panicum* species (Gramineae). *Hawaiian plant studies* **149**. *Phytologia* **63**: 368-395. 1987. [Many new species in various groups; illustrations fairly good.]
- SCHMOLL, H. M. A realignment of the *Panicum thermale* group. *Madroño* **5**: 90-96. 1939. [Western North American members of subg. *Dichantherium*.]
- SCHOLZ, H. Flaschenförmige Mikrohaare in der Gattung *Panicum* (Gramineae). *Willdenowia* **8**: 511-515. 1979. [Scanning electron micrographs of modified bicellular microhairs in several species of *Panicum*.]
- SENECA, E. D. Germination response to temperature and salinity of four dune grasses from the Outer Banks of North Carolina. *Ecology* **50**: 45-53. 1969. [*P. amarum*.]
- . Seedling response to salinity in four dune grasses from the Outer Banks of North Carolina. *Ecology* **53**: 465-471. 1972. [*P. amarum*.]
- , W. W. WOODHOUSE, & S. W. BROOME. Dune stabilization with *Panicum amarum* along the North Carolina coast. U.S. Army Corps Engineers, Coastal Engineering Res. Center, Misc. Rep. No. 76-3. 42 pp. 1976.
- SHARMA, M. The genus *Panicum* Linn. in Punjab (India). *Jour. Econ. Taxon. Bot.* **7**: 103-109. 1985. [Key, descriptions.]
- SHERIF, A. S. *Panicum sphaerocarpon* Ell. var. *polyanthes* (Schultes) A. S. Sherif (Poaceae) comb. nov. *Sida* **10**: 191. 1983.
- SHETTY, S. A., & H. S. SHETTY. Role of *Panicum trypheron* in annual recurrence of false smut of rice. *Trans. Brit. Mycol. Soc.* **88**: 409-411. 1987. [*P. trypheron* serves as a source of inoculum between growing seasons.]
- SILL, W. H., & R. C. PICKETT. A new virus disease of switchgrass, *Panicum virgatum* L. *Pl. Disease Rep.* **41**: 241-249. 1957. [*Panicum* mosaic virus; capable of infecting species of *Panicum*, *Digitaria*, *Setaria*, *Echinochloa*.]
- SISSON, W. B. Carbon balance of *Panicum coloratum* during drought and non-drought in the northern Chihuahuan desert. *Jour. Ecol.* **77**: 799-810. 1989.
- SKOTTSBERG, C. Chromosome numbers in Hawaiian flowering plants. *Ark. Bot.* **II**. **3**: 63-70. 1953. [All Hawaiian *Panicum* species reported are $2n = 18$.]
- SPELLENBERG, R. In: IOPB chromosome number reports. XXV. *Taxon* **19**: 102-113. 1970a. [Eight species; all $n = 9$ or $2n = 18$.]
- . *Panicum shastense* (Gramineae), a sterile hybrid between *P. pacificum* and *P. Scribnerianum*. *Brittonia* **22**: 154-162. 1970b.
- . Autogamy and hybridization as evolutionary mechanisms in *Panicum* subgenus *Dicantherium* [sic] (Gramineae). *Brittonia* **27**: 87-95. 1975a.
- . Synthetic hybridization and taxonomy of western North American *Dichantherium*, group *Lanuginosa* (Poaceae). *Madroño* **23**: 134-153. 1975b.
- STEPHENSON, S. N. The genus *Dichantherium* (Poaceae) in Michigan. *Michigan Bot.* **23**: 107-119. 1984. [Good regional treatment.]
- STEYERMARK, J. A., & H. M. SCHMOLL. *Panicum Tuckermanni*, a variety of *Panicum philadelphicum*. *Rhodora* **41**: 86-90. 1939. [Now usually considered a distinct species.]

- STRID, A. In: IOPB chromosome number reports. LXIX. Taxon **29**: 703-730. 1980. [*P. miliaceum*, $2n = 36$.]
- SWALLEN, J. R. The *Latissima* group of *Panicum*. Sellowia **18**: 109-113. 1966. [Brazilian.]
- THOMASSON, J. R. Observations on the characteristics of the lemma and palea of the late Cenozoic grass *Panicum elegans*. Am. Jour. Bot. **65**: 34-39. 1978.
- . Miocene grass fossils: possible adaptation in reproductive bracts (lemma and palea). Ann. Missouri Bot. Gard. **72**: 843-851. 1985.
- VOSS, E. G. Additional nomenclatural and other notes on Michigan monocots and gymnosperms. Michigan Bot. **11**: 26-37. 1972. [Comments on typification in *Panicum*, noting the error in typification of *P. latifolium* L. by BAUM (1967).]
- . Michigan Flora. Part I. Gymnosperms and Monocots. Cranbrook Inst. Sci. Bull. **55**. color frontisp. + viii + 488 pp. Bloomfield Hills, Mich. 1972. [*Panicum*, 223-238.]
- WALLACE, L. L. Growth, morphology and gas exchange of mycorrhizal and nonmycorrhizal *Panicum coloratum* L., a C_4 grass species, under different clipping and fertilization regimes. Oecologia **49**: 272-278. 1981.
- WARNER, D. A., M. S. B. KU, & G. E. EDWARDS. Photosynthesis, leaf anatomy, and cellular constituents in the polyploid C_4 grass *Panicum virgatum*. Pl. Physiol. **84**: 461-466. 1987.
- WARWICK, S. I. Isozyme variation in proso millet. Jour. Hered. **78**: 210-212. 1987. [Considerable morphological and physiological variation not paralleled by isozyme variation; most loci show little or no variation.]
- WILCUT, J. W., R. R. DUTE, B. TRUELOVE, & D. E. DAVIS. Factors limiting the distribution of cogongrass, *Imperata cylindrica*, and torpedograss, *Panicum repens*. Weed Sci. **36**: 577-582. 1988a. [Rhizomes of *P. repens* tolerant of desiccation.]
- , B. TRUELOVE, D. E. DAVIS, & J. C. WILLIAMS. Temperature factors limiting the spread of cogongrass (*Imperata cylindrica*) and torpedograss (*Panicum repens*). Ibid. 49-55. 1988b. [*P. repens* susceptible to cold temperatures.]
- WILLIAMS, J. T., & R. M. FARIAS. Utilisation and taxonomy of the desert grass *Panicum turgidum*. Econ. Bot. **26**: 13-20. 1972.
- WILSON, J. R., R. H. BROWN, & W. R. WINDHAM. Influence of leaf anatomy on the dry matter digestibility of C_3 , C_4 , and C_3/C_4 intermediate types of *Panicum* species. Crop Sci. Madison **23**: 141-146. 1983. [Plants of C_3 species are most digestible.]
- WRIGHT, L. N. Germination rate and growth characteristics of blue panicgrass. Crop Sci. Madison **20**: 42-44. 1980. [= *P. antidotale* Retz.]
- ZHANG, J., & M. A. MAUN. Seed dormancy of *Panicum virgatum* L. on the shoreline sand dunes of Lake Erie. Am. Midl. Nat. **122**: 77-87. 1989.
- ZULOAGA, F. O. El género *Panicum* (Gramineae) en la República Argentina. I. Darwiniana **22**: 3-44. 1979. [Sectional key; excellent illustrations.]
- . Notas sinonímicas en el género *Panicum* (Gramineae). Ibid. **23**: 639-649. 1981. [Central and South American species; descriptions, excellent illustrations.]
- . El género *Panicum* (L.) sección *Parviglumia*. Ibid. **26**: 353-369. 1985. [Central and South American group; key, descriptions, excellent illustrations.]
- . El género *Panicum* (Poaceae: Paniceae) sect. *Cordovensia*. Ibid. **27**: 403-429. 1986. [South American section of subg. *Dichanthelium*; key, descriptions, excellent illustrations, scanning electron micrographs of distal floret characters.]
- . Systematics of New World species of *Panicum* (Poaceae: Paniceae). Pp. 287-306 in T. R. SODERSTROM *et al.*, eds., Grass systematics and evolution. Washington, D.C. 1987a. [Six subgenera, 25 sections in the Americas.]
- . A revision of *Panicum* subgenus *Panicum* section *Rudgeana* (Poaceae: Paniceae). Ann. Missouri Bot. Gard. **74**: 463-478. 1987b. [Neotropical group;

good table summarizing distribution of character states in sections of subgenera *Phanopyrum*, *Dichanthelium*, *Agrostoides*, and *Panicum* and in *Yakirra*.]

— & T. SENDULSKY. A revision of *Panicum* subgenus *Phanopyrum* section *Stolonifera* (Poaceae: Paniceae). Ann. Missouri Bot. Gard. **75**: 420–455. 1988. [Neotropical group.]

8. *Lasiacis* (Grisebach) Hitchcock, Contr. U.S. Natl. Herb. **15**: 16. 1910.

Caespitose [rhizomatous, stoloniferous, or decumbent] perennials [annuals]. Stems woody [herbaceous], sometimes exceeding 3 m in height, scandent [prostrate], branched above, upper portions of stem often zigzag; internodes hollow [solid]; nodes glabrous (puberulent). Leaves with sheaths pubescent on margins; ligule a fringed or unfringed membrane; blades linear-lanceolate to ovate or elliptic, flat, glabrous or scabrous to pubescent, acute to acuminate at apex, cuneate or cordate at base, often pseudopetiolate, rolled in bud, lower blades often disarticulating from sheaths; photosynthesis C_3 . Inflorescences paniculate, open [contracted], branches spreading or reflexed, terminating in spikelets. Spikelets terete, disarticulating below the glumes, adaxial, obliquely attached to pedicels (pedicel apices truncate or cupuliform), black at maturity, solitary; proximal florets sterile [staminate], paleate, [two sterile florets below perfect floret in *L. anomala*]; with or without rachilla prolonged apically. Calli undifferentiated. Glumes 2, unequal, chartaceous, ovate, apiculate; proximal glumes shorter than distal glumes, with tufts of hairs at apex, [5] 7–13 nerved, encircling spikelet base; distal glumes equalling proximal lemmas, [7] 9–13 [15] nerved. Proximal lemmas equalling and less firm than distal lemmas, awnless, [7] 9–13 [15] nerved; distal lemmas obovoid, indurate, smooth, whitish to brown, obtuse, with tufts of white hairs at apex, 7 nerved, with involute margins and conspicuous germination flap. Distal paleas indurate, gibbous and with tufts of hairs at apex, 2 keeled. Lodicules 2. Ovaries with styles free, stigmas white or purple. Caryopses (grains) small, longitudinally grooved or not, smooth; pericarp thin; endosperm hard. Base chromosome number 9. LECTOTYPE SPECIES: *Lasiacis divaricata* (L.) Hitchc.; see Hitchcock & Chase, Contr. U.S. Natl. Herb. **15**: 16. 1910. (Name from Greek, *lasios*, woolly, and *akis*, point, referring to the tuft of woolly hairs at the apex of the glumes and lemmas.) — SMALL CANE, TIBISEE.

A genus of 16 species of forests and forest edges in the Neotropics, including southern Florida, the West Indies, Mexico, and Central America, southward to southern Peru and northern Argentina. Two species, *L. divaricata* (L.) Hitchc., small cane, Florida tibisee, $n = 18$, (leaves generally less than 2 cm wide, linear-lanceolate, spikelets more than 4 mm long, inflorescence branches sparsely flowered) and *L. ruscifolia* (Kunth) Hitchc., $n = 18$, (leaves more than 2 cm wide, often pubescent, lance-ovate to ovate, spikelets less than 4 mm long, inflorescence branches with numerous densely arranged spikelets) occur in

our area. They are restricted to southern Florida (Davidse, 1978; Wunderlin). Davidse (1978) recognized three varieties within *L. divaricata*, but only *L. divaricata* var. *divaricata* occurs in Florida. *Lasiacis ruscifolia* contains two varieties, of which only var. *ruscifolia* is known in Florida (Davidse, 1978).

Lasiacis was described originally as a section of *Panicum* (Grisebach). However, Hitchcock (in Hitchcock & Chase, 1910) elevated it to generic rank on the basis of its several very distinctive features, including the woody, bamboo-like stems of many species, globose spikelets set obliquely on pedicels, indurate distal lemmas, downy tufts at the apices of the spikelet bracts, and gibbous palea apices. *Lasiacis* has palisade chlorenchyma in its leaves, a feature unique in the Paniceae, and found elsewhere within the Gramineae only in tribe Centothecae Ridley (Davidse, 1978; Davidse *et al.*, 1986).

Most authors now agree that *Lasiacis* is a distinct genus. It contains only neotropical species in Davidse's circumscription (1978). However, Clayton & Renvoize considered the Madagascan-Comoran species described by Camus under *Pseudolasiacis* (1926, 1945) to belong in *Lasiacis*. Davidse (1978) did not mention these, and also did not discuss the status of *Pseudolasiacis*, even in the context of its relationship to *Lasiacis* and other genera.

The spikelet structure of *Lasiacis* is based on a *Panicum* theme. *Panicum* also emerges as most similar to *Lasiacis* in the phenetic analysis of Watson & Dallwitz, with *Ichnanthus*, *Acroceras*, and *Ancistrachne* S. T. Blake. However, Davidse (1978) implicitly agreed with Hsu's (1965) and Butzin's (1970) interpretations of relationships, whereby *Lasiacis* is aligned with *Acroceras* (and *Commelinidium* Stapf, if maintained as distinct from *Acroceras*) and other genera in Butzin's subtribe Microcalaminae, rather than with *Panicum* and its allies. Hsu, Butzin, and Davidse believe that *Lasiacis* is one of the most primitive members of the Paniceae, but the evidence for this is scant. Monophyly of subtribe Microcalaminae has not been demonstrated.

Lasiacis anomala Hitchc. is unusual in the genus, and in tribe Paniceae in general, in having two sterile lemmas below the distal fertile lemma. Considering that this feature is found only in plants within a restricted range (north-central South America and some of the islands of the Lesser Antilles), Hitchcock (1919) concluded that it should be recognized as a species distinct from the closely related *L. ruscifolia*, and Davidse (1978) concurred. The occurrence of an extra sterile lemma is known elsewhere in the Paniceae only in *Panicum quadriglume* (Doell) Hitchc. Clayton & Renvoize (p. 275) suggested that this condition reflects "...residual genetic mutability in the panicoid spikelet..."

All species of *Lasiacis* are basically tetraploid ($n = 18$), with only one diploid count having been reported ($n = 9$ in *L. sorghoidea* (Desv.) Hitchc. & Chase from Colombia; Gould & Soderstrom, 1970b). All species for which compatibility data are available are self-compatible, and inbreeding predominates. Anthers and stigmas become exerted

and are mature or receptive simultaneously (Davidse, 1978; Davidse & Morton).

The spikelets of *Lasiacis* are unique among the panicoids in that they mature into black, berry-like structures at maturity. The inner epidermis of each spikelet bract is modified for lipid production, and the thick distal lemma and palea provide protection for the seed. These spikelet modifications are all geared toward bird attraction and subsequent dispersal of the seeds. Examinations of stomach contents and observations in the field confirm that frugivorous and omnivorous birds utilize these fruits, and that granivorous birds are not attracted to them. Presumably, birds derive nourishment from the lipids. Germination experiments with seeds that have passed through the digestive tracts of birds indicate that the seeds remain viable (Davidse & Morton).

Species of *Lasiacis* are of little economic importance. *Lasiacis divaricata* and *L. procerrima* Hitchc. have been used in the preparation of diuretics, antiseptics, and remedies for seasickness and kidney pain in South America (Morton). Holm *et al.* list *L. ligulata* Hitchc. & Chase and *L. ruscifolia* as weeds in Peru, and in Puerto Rico and the Dominican Republic, respectively.

REFERENCES:

- Under references for tribe see BOLKHOVSKIKH *et al.*; BUTZIN (1970); CHASE (1911); CLAYTON & RENVOIZE; GOULD (1979); GOULD & SODERSTROM (1967, 1970b); HITCHCOCK & CHASE (1910); HOLM *et al.*; HSU (1965); MORTON; POHL (1980); WATSON & DALLWITZ; WEBSTER (1988); and WUNDERLIN.
- CAMUS, A. *Panicum* nouveaux de la section *Pseudolasiacis* A. Camus. Bull. Soc. Bot. France **73**: 974-977. 1926.
- . Sur la présence de nervures tessellées dans les feuilles de Graminées. Bull. Mens. Soc. Linn. Soc. Bot. Lyon **14**: 70-73. 1945. [*Pseudolasiacis* similar to but distinct from *Lasiacis* in leaf characters.]
- DAVIDSE, G. A new species of *Lasiacis* (Gramineae). Phytologia **29**: 152, 153. 1974. [*L. nigra*.]
- . New taxa and combinations in the genus *Lasiacis* (Gramineae). Ann. Missouri Bot. Gard. **64**: 374, 375. 1977.
- . A systematic study of the genus *Lasiacis* (Gramineae: Paniceae). *Ibid.* **65**: 1133-1254. 1978. [Excellent monograph.]
- & E. MORTON. Bird-mediated fruit dispersal in the tropical grass genus *Lasiacis* (Gramineae: Paniceae). Biotropica **5**: 162-167. 1973.
- , T. R. SODERSTROM, & R. P. ELLIS. *Pohlidium petiolatum* (Poaceae: Centothecae), a new genus and species from Panama. Syst. Bot. **11**: 131-144. 1986. [*Lasiacis* the only non-centothecoid grass with palisade chlorenchyma.]
- GRISEBACH, A. H. R. Flora of the British West Indian Islands. London. 1864. [Description of *Panicum* sect. *Lasiacis*, with five spp., 551.]
- HITCHCOCK, A. S. A peculiar species of *Lasiacis*. Jour. Wash. Acad. Sci. **9**: 35-38. 1919. [Two sterile lemmas in *L. anomala*.]
- . The North American species of *Lasiacis*. Contr. U.S. Natl. Herb. **22**: 13-31. 1920. [Fifteen spp.]

9. *Amphicarpum* Kunth, R v. Gram. 1(2): 28. 1829.

Erect or decumbent perennials or annuals. Stems 30–100 cm high, branching at lower nodes; internodes hollow; nodes glabrous or pubescent. Leaves with sheaths glabrous or pubescent, margins ciliate; ligule a fringe of hairs; blades linear to lanceolate, flat, glabrous to hispid, with truncate or rounded bases, margins cartilaginous; photosynthesis C_3 . Inflorescences paniculate, with ascending aerial branches terminating in chasmogamous spikelets, and short subterranean branches terminating in single cleistogamous spikelets. Spikelets dorsiventrally compressed, disarticulating below the glumes (or at base in subterranean shoots with cleistogamous spikelets), adaxial, pedicellate (pedicel apices cupuliform), solitary; proximal florets neuter, epaleate. Calli undifferentiated. Glumes 1 or 2 (proximal glume, when present on aerial spikelets, minute, hyaline, nerveless), distal glumes equalling or shorter than lemmas, acuminate, awnless, 5–7 nerved. Proximal lemmas equalling or shorter and less firm than distal lemmas, acuminate, awnless; distal lemmas chartaceous, indurate, pubescent when young, acuminate, with flat margins and conspicuous germination flap. Distal paleas indurate, awnless. Lodicules 2. Ovaries with styles free, stigmas red to purple. Base chromosome number 9. TYPE SPECIES: *Amphicarpum Purshii* Kunth, the only species included in the genus at the time of its original description. (Name from Greek *amphicarpos*, doubly fruit-bearing, referring to the two types of inflorescences produced by this plant.) — MAIDENCANE, PEANUTGRASS.

A genus of two species endemic to the Coastal Plain of the eastern United States and growing in openings in moist grasslands, pine barrens, woods, and disturbed areas. Both species occur in the Southeast. *Amphicarpum Purshii* Kunth, $2n = 18$, is known from New Jersey to South Carolina. It has been reported from Georgia, but the recent atlas of vascular plants of Georgia does not include it (Jones & Coile). *Amphicarpum Purshii* has densely hispid leaves and sheaths and aerial spikelets 4–5.5 mm long. *Amphicarpum Muhlenbergianum* (Schultes) Hitchc. (*A. floridanum* Chapman), blue maidencane, $2n = 18$, occurs mainly in Florida, although there are a few records from South Carolina (Radford *et al.*) and Alabama (Lelong, 1988). Its leaves are glabrous, although the sheath margins may be ciliate, and the aerial spikelets are 6–7.5 mm long.

Amphicarpum is similar to *Panicum* and differs from it mainly in its subterranean cleistogamous spikelets, reduced proximal glumes, and scattered hairs on the distal lemma. This last feature is rare in the Paniceae, occurring elsewhere only in the African-Australian genus *Entolasia* Stapf and in the Australian genus *Cleistochloa* C. E. Hubb. (Webster, 1988). The nearest-neighbor analysis of Watson & Dallwitz also indicates that *Panicum* is phenetically most similar to *Amphicarpum*, as well as to *Scutachne* Hitchc. & Chase (West Indies) and *Yakirra*

(Australia). However, *Stipa* L. (subfam. Arundinoideae) is also similar in that analysis, clearly an erroneous result and emphasizing the potential pitfalls of reliance on phenetic analyses for indications of relationship.

The interesting reproductive biology of *Amphicarpum* has been the focus of several ecological investigations. In *A. Purshii* aerial and subterranean flowers are self-fertile, but only aerial flowers are capable of cross-pollination (Cheplick & Quinn, 1988; McNamara & Quinn; Weatherwax). Nevertheless, only 19 of 60 quantitative characters showed significant phenotypic variation in progeny raised from aerial flowers, indicating that considerable self-fertilization is occurring in these flowers. Also, fitness traits (e.g., seed set, seed weight) showed the least amount of genetic variation. *Amphicarpum Purshii* also exhibits shifts in the ratio of aerial to subterranean seed production. As succession proceeds, or disturbance diminishes, this ratio declines, and the number of propagules in the seed bank rises. Allocation of resources to aerial seeds diminishes, but a source of subterranean propagules has accumulated and is available for the onset of another episode of disturbance (Cheplick & Quinn, 1983). The allocation of energy to propagules in *A. Purshii* appears to be comparable to allocations in other amphicarpic annuals from diverse plant groups.

REFERENCES:

Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; CLAYTON & RENVOIZE; CLEWELL; JONES & COILE; LELONG (1988); RADFORD *et al.*; WATSON & DALLWITZ; WEBSTER (1988); and WUNDERLIN.

CHASE, A. Notes on cleistogamy of grasses. *Bot. Gaz.* **45**: 135, 136. 1908.

CHEPLICK, G. P. Nutrient availability, dimorphic seed production, and reproductive allocation in the annual grass *Amphicarpum Purshii*. *Canad. Jour. Bot.* **67**: 2514-2521. 1989. [Early subterranean seed production provides a nearly guaranteed reproductive mechanism, and aerial sexual reproduction provides a means of increased reproductive output when conditions are favorable.]

—— & J. A. QUINN. *Amphicarpum Purshii* and the "pessimistic strategy" in amphicarpic annuals with subterranean fruit. *Oecologia* **52**: 327-332. 1982.

—— & ———. The shift in aerial/subterranean fruit ratio in *Amphicarpum Purshii*: causes and significance. *Ibid.* **57**: 374-379. 1983.

—— & ———. Self-fertilization in *Amphicarpum Purshii*: its influence on fitness and variation of progeny from aerial panicles. *Am. Midl. Nat.* **116**: 394-402. 1986.

—— & ———. Quantitative variation of life history traits in amphicarpic peanut-grass (*Amphicarpum Purshii*) and its evolutionary significance. *Am. Jour. Bot.* **75**: 123-131. 1988.

GRAY, J. R., & D. E. FAIRBROTHERS. A clarification of some misconceptions about *Amphicarpum Purshii* (Gramineae). *Bull. Torrey Bot. Club* **98**: 174, 175. 1971. [Morphology, reproductive biology.]

HOLM, T. A study of some anatomical characters of North American Gramineae. VII. The genus *Amphicarpum*. *Bot. Gaz.* **22**: 403-406. 1896. [Separation of *A. Purshii* and *A. Muhlenbergianum*.]

MCMANARA, J., & J. A. QUINN. Resource allocation and reproduction in populations of *Amphicarpum Purshii* (Gramineae). *Am. Jour. Bot.* **64**: 17-23. 1977.

WEATHERWAX, P. Flowering and seed production in *Amphicarpum floridanum*. Bull. Torrey Bot. Club 61: 211–215. 1934.

10. *Hymenachne* Palisot de Beauvois, Essai Agrost. 48. 1812.

Stoloniferous perennials. Stems 50–200 cm high, branched; internodes solid or spongy; nodes glabrous. Leaves with sheaths glabrous except along margins; ligule a fringed or unfringed membrane; blades linear to lanceolate, flat, cordate [rounded] at base, glabrous except along margins near base, with or without readily visible transverse veins; photosynthesis C_3 . Inflorescences paniculate, cylindrical, with spike-like or more freely branched primary branches and appressed secondary branches terminating in spikelets, spikelets dense. Spikelets lanceolate, dorsiventrally compressed, disarticulating below the glumes, adaxial, secund, short-pedicellate (pedicel apices truncate or discoid), solitary; proximal florets sterile, epaleate; rachilla pronounced between glumes. Calli undifferentiated. Glumes 2, unequal; proximal glumes shorter than distal glumes, acute to acuminate, 3–5 nerved, encircling spikelet base; distal glumes equalling proximal lemmas or nearly so, [3] 5 [7] nerved. Proximal lemmas equalling or exceeding and similar in texture to or less firm than distal lemmas, acute to short awned, [3] 5 nerved; distal lemmas membranaceous to chartaceous, smooth to scabrous, glabrous, white, dull, acute, awnless, 2 or 3 nerved, with flat, thin margins and conspicuous germination flap. Distal paleas membranaceous, gaping. Lodicules 2. Ovaries with styles fused. Caryopses (grains) small, not grooved, smooth. Base chromosome number 10. LECTOTYPE SPECIES: *Hymenachne monostachya* (Poiret) Beauv. = *H. amplexicaulis* (Rudge) Nees; see Chase, Proc. Biol. Soc. Wash. 24: 146. 1911. (Name from Greek, *hymen*, membrane, and *achne*, chaff, referring to the membranaceous distal floret bracts.)

A pantropical genus of about five species of wetlands. One species, *H. amplexicaulis*, $n = 10$, $2n = 20$, has become naturalized in southern Florida in wet pastures, where it is rare. Webster (1987) lists *H. amplexicaulis* as a synonym of *H. acutigluma* (Steudel) Gilliland, but since the basionym of the former predates that of the latter by almost 50 years, the reason for doing this is obscure. Both names are in the literature treating the flora of the southeastern United States (e.g., Webster, 1988; Wunderlin). *Panicum hemitomon*, which occurs on the Coastal Plain from New Jersey southward to Florida and Texas, was placed in *Hymenachne* by Hsu (1965), primarily on the basis of vegetative characters. Since its reproductive features are similar to those of *Panicum*, subsequent authors have not accepted Hsu's transfer.

Hymenachne is thought to be related to *Sacciolepis* Nash and *Panicum* (Clayton & Renvoize; Pohl, 1980; Pohl & Lersten; Simon). Watson & Dallwitz and Webster (1988) note similarities to *Digitaria*, *Alloteropsis*, *Homopholis* C. E. Hubb. and/or *Poecilostachys* Hackel. However, the base chromosome number of *Alloteropsis* and *Digitaria*

is nine (chromosome numbers are unknown in *Homopholis* and *Poecilostachys*), whereas it is ten in *Hymenachne*. Clayton & Renvoize note that *Hymenachne* contains species that are difficult to distinguish from certain species of *Panicum* (e.g., *P. rivulare* Trin.), and early authors (Bentham, Hackel) classified it as a section of *Panicum*. In Butzin's artificial classification system (1970), *Hymenachne* is put in subtribe Microcalaminae with all other genera of Paniceae with leaf cross-veins in the leaves. He claimed that this subtribe was held together by other characters as well, but mentioned none that could be construed as definitive.

Prior to anatomical investigations, *Hymenachne* and *Sacciolepis* were distinguished solely on the basis of the presence or absence of a saccate distal glume. Pohl & Lersten discovered that the pith anatomy also differs. *Hymenachne* consistently has specialized aerenchyma tissue in the internodal regions of the stem. Haynes conducted a detailed examination of this tissue in *H. amplexicaulis*. *Sacciolepis*, in contrast, has hollow internodes. Pohl & Lersten also noted that the leaf epidermis in *Hymenachne* bears prickly cells, whereas this type of cell is absent in *Sacciolepis*. On the basis of incorrect internode anatomy, spikelet morphology, and inflorescence structure, three anomalous species placed in *Hymenachne* by some authors (*H. condensata* (Bertol.) Chase, *H. montana* (Griseb.) Hackel, *H. hemitomom* (Schultes) Hsu) do not belong in this genus, but Pohl & Lersten fail to state where these species should be placed. As noted above, *H. hemitomom* (Schultes) C. Hsu belongs in *Panicum*, but the disposition of the other two is unsettled.

Hymenachne amplexicaulis forms a part of the floating islands in the Amazon River (Roshevits). The aerenchymatous tissue of the stem internodes may provide buoyancy, structural support, and an oxygen transport system (Haynes). Species of *Hymenachne* appear to have few specializations for diaspore dispersal, although the ability of this perennial to root at the nodes (Roshevits) indicates the likelihood of an efficient means of vegetative dispersal. Long-distance dispersal may be facilitated by moving water or by mud containing fruits adhering to the feet of aquatic birds (Davidse, 1987), but no observational or experimental evidence in favor of this suggestion exists, as yet.

Hymenachne amplexicaulis is considered to be a weed in Surinam, Trinidad, and Indonesia (Holm *et al.*).

REFERENCES:

Under references for tribe see BENTHAM; BUTZIN (1970); CHASE (1911); CLAYTON & RENVOIZE; DAVIDSE (1987); HACKEL; HOLM *et al.*; HSU (1965); POHL (1980); POHL & LERSTEN; ROSHEVITS; SIMON; WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.

HAYNES, J. L. The anatomy of anomalous grass *Hymenachne amplexicaulis*. Proc. Indiana Acad. Sci. 44: 69-72. 1934.

SCHLECHTENDAL, D. F. L. VON. Die Gattung *Hymenachne* Pal. Beauv., in Betrachtung gezogen. Linnaea 31: 348-370. 1861. [All taxa discussed under

the names of the genera in which they were originally described; thus, no new combinations.]

11. *Sacciolepis* Nash in Britton, Man. Fl. North. U.S. 89. 1901.

Decumbent or caespitose [rhizomatous, stoloniferous] perennials or annuals. Stems unbranched [branched above], to 10 [15] dm tall; internodes hollow; nodes glabrous. Leaves with sheaths glabrous [pubescent], not auriculate [auriculate]; ligule a fringed membrane; blades linear, flat [folded, rolled], glabrous or pubescent [papillose], with truncate to rounded base, with or without conspicuous transverse veins, rolled in bud; photosynthesis C_3 . Inflorescences paniculate, contracted [open], primary branches with appressed secondary branches terminating in spikelets. Spikelets dorsiventrally to laterally compressed, disarticulating below the glumes (also below distal lemma), adaxial, short-pedicellate (pedicel apices discoid), solitary; proximal florets staminate or sterile, paleate or epaleate. Calli undifferentiated. Glumes 2, unequal, glabrous or pubescent, acute to obtuse, awnless; proximal glumes shorter than distal glumes, 3–7 nerved, not encircling spikelet base; distal glumes distinctly saccate, [5] 7–9 [13] nerved. Proximal lemmas exceeding and less firm than distal lemmas, glabrous or pubescent, obtuse to acuminate, awnless, 5–7 nerved; distal lemmas cartilaginous, smooth, glabrous, lustrous [dull], acute, awnless, 3–5 nerved, with involute margins and conspicuous germination flap. Distal paleas indurate or not, awnless, 2 nerved, not fully enclosed by distal lemmas. Lodicules 2. Ovaries with styles free. Caryopses (grains) small, not grooved, smooth; pericarp thin; endosperm hard, without lipid. Base chromosome number 9. TYPE SPECIES: *Sacciolepis gibba* (Ell.) Nash = *S. striata* (L.) Nash, the only species included in the genus at the time of its original description. (Name from Greek, *sakkos*, bag, and *lepis*, scale, in reference to the gibbous or saccate distal glume.) — CUPSCALE.

A genus of about 30 species occurring in wetlands, moist open woodlands, in ditches, and along roadsides throughout the tropics. Africa (especially Southeast Africa and West Africa) is the center of diversity; approximately 25 species occur on that continent (Simon). There is no comprehensive monograph for the entire genus. The only recent revisionary work is that of Simon, who treated 16 species in the *Flora Zambesiaca* area (parts of Namibia, Botswana, Zimbabwe, Zambia, Malawi, and Mozambique). Stapf (1919–1934) described *Rhampholepis*, but later in the same work, he merged it with *Sacciolepis* Nash and treated it as a section. However, it seems that no one else has taken up his suggestion to subdivide *Sacciolepis*.

Two species of *Sacciolepis*, neither of which is among the taxa revised by Simon, occur in the Southeast. *Sacciolepis indica* (L.) Chase, India cupscale, $n = 9$, 18 (annual, caespitose, stems to 1.5 dm tall, leaves 3–6 mm wide, spikelets to 3 mm long) is a weedy adventive from India.

It grows in moist to wet, disturbed habitats in Florida, Georgia, North Carolina, Mississippi, and Texas. *Sacciolepis striata* (L.) Nash, American cupscale, $2n = 36$ (perennial, stoloniferous, to 10 dm tall, leaves 6–15 mm wide, spikelets 3.5–5 mm long) occurs in natural wetlands such as marshes, swamps, lake and stream edges, and wet hammocks, and also in moist, disturbed ditches, from New Jersey to Florida and Texas, mainly on the Coastal Plain, but also in southern and central Arkansas and in Tennessee (Blomquist; Radford *et al.*; E. Smith).

Species of *Sacciolepis* were included originally in *Panicum*, and this is an appropriate reflection of its relationship. Distinguishing characters of *Sacciolepis* include gibbous or saccate distal glumes, strongly nerved distal glumes and proximal lemmas, relatively short, glossy distal lemmas (without distinctly involute margins), and minute filiform stipes at the base of the distal florets (Simon; Webster, 1987, 1988). Watson & Dallwitz indicated that *Arthragrostis* Lazarides, *Panicum*, *Ichnanthus*, and *Setaria* are most similar phenetically. Webster (1988) noted that the filiform stipes that subtend the distal florets suggest a close relationship with *Ichnanthus*, and that the contracted panicle recalls *Hymenachne*. Simon supports the idea of a close relationship among *Sacciolepis*, *Ichnanthus*, *Panicum*, *Hymenachne*, and *Setaria*, but he also concluded that *Thyridachne* C. E. Hubb., *Hydrothauma* C. E. Hubb., and *Cyrtococcum* Stapf are close relatives.

The relationship between *Sacciolepis* and *Hymenachne* has been the subject of close scrutiny. Some species in each genus are difficult to assign on the basis of the degree to which the distal glume is gibbous. Also, both genera have similar contracted panicles and similar preferences for moist to wet habitats. Anatomical differences between these genera are discussed under the treatment of *Hymenachne* (see Pohl & Lersten).

Bor (1960) has suggested that the fruits of *Sacciolepis interrupta* (Willd.) Stapf may be dispersed by water, although the mechanism by which this would be accomplished was not discussed. Davidse (1987) speculated that in wetland genera, such as *Sacciolepis*, without any obvious modifications for propagule dispersal, fruit (along with mud) adhering to the feet of aquatic birds might be the dispersal mechanism.

Sacciolepis interrupta is considered to be a relatively significant weed in Nigeria, and six other species are weeds of unspecified importance (Holm *et al.*). None of the species of *Sacciolepis* is an important forage crop.

REFERENCES:

- Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; BOR (1960); CHIPPINDALL; CLAYTON & RENOVOISE; CLEWELL; DAVIDSE (1987); GOULD (1975, 1979); HOLM *et al.*; JONES & COILE; MACROBERTS; POHL & LERSTEN; RADFORD *et al.*; SIMON; E. SMITH; STAPF (1919–1934); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.

AHLES, H. E., & A. E. RADFORD. Species new to the flora of North Carolina. Jour. Elisha Mitchell Sci. Soc. **75**: 140–147. 1959. [*S. indica*, Sampson Co.]

KYODA, K. A new record to grass flora of Japan, a panicoid C₃ species, *Sacciolepis myosuroides*. Jour. Jap. Bot. 63: 102-110. 1988.

12. *Echinochloa* Palisot de Beauvois, Essai Agrost. 53. 1812.

Decumbent or caespitose annuals or perennials. Stems 40-360 [450] cm high, branched or unbranched above, from tuberous or non-tuberous bases; internodes spongy (aerenchymatous); nodes glabrous to minutely puberulent. Leaves with sheaths compressed, glabrous to papillose-pubescent; ligule absent or a fringe of hairs; blades linear, flat, glabrous to scabrous or pubescent, with incised bases; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences paniculate, with 1-many, often secund spike-like primary branches (occasionally also with appressed or ascending secondary branches) terminating in spikelets. Spikelets dorsiventrally compressed, disarticulating below the glumes, adaxial, secund, subsessile or pedicellate (pedicel apices truncate, discoid, or cupuliform), solitary or paired; proximal florets staminate or neuter, paleate (epaleate in some forms of *E. crusgavonis*). Calli undifferentiated. Proximal glumes shorter than distal glumes, awnless to short-awned, 0-3 nerved, encircling spikelet base; distal glumes equalling proximal lemmas, glabrous to long-scabrous, awned or mucronate, [3] 5-9 nerved. Proximal lemmas similar in texture or less firm than distal lemmas, glabrous to long-scabrous, awned or awnless, 5 nerved; distal lemmas indurate, smooth, lustrous, glabrous (some taxa with a narrow zone of minute hairs near apex), mucronate or awned, 5 nerved, with involute margins and conspicuous germination flap. Distal paleas indurate, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red. Caryopses (grains) smooth; endosperm hard, without lipid, containing only simple starch grains. Base chromosome number 9. LECTOTYPE SPECIES: *Echinochloa crusgalli* (L.) Beauv.; see Chase, Proc. Biol. Soc. Wash. 24: 154. 1911. (Name from Greek, *echinos*, hedgehog, and *chloë*, grass, referring to the spinulose spikelets of many species.) — COCKSPUR, JUNGLE-RICE, BARNYARD GRASS, JAPANESE MILLET, BILLION-DOLLAR GRASS.

Twenty to 40 species of wetlands, cultivated fields, and wet or dry disturbed woodlands and grasslands in the tropical and temperate zones of the world. Seven species occur in North America and the Southeast. Phenotypic plasticity in vegetative and some spikelet characters (e.g., awns and pubescence) is exhibited by many species. As a result, taxonomic treatments have varied considerably, and species problems in *Echinochloa* are considered the most difficult of any in the smaller panicoid genera (Webster, 1988). No infrageneric taxa above species are recognized.

The most distinctive features of *Echinochloa* are the smooth distal floret, lack of bristles subtending the spikelets, incised leaf blade bases, and the differentiation of the distal lemma apex into a green, sometimes

wrinkled point. Many species have coarse hairs on the spikelets and panicle branches.

On the basis of common features of morphology, anatomy, and cytology, *Echinochloa* is evidently closely related to *Panicum*. However, Watson & Dallwitz's analysis of phenetic relationships suggests a closer morphological resemblance to *Paspalum*, *Brachiaria* (= *Urochloa*, p.p.), *Paspalidium*, and *Setaria*. Tsvelev (1976) also aligned *Echinochloa* with several of these genera (*Brachiaria*, *Paspalum*), in subtribe Brachiariinae. His subtribal classification closely follows that of Butzin (1970) and is more finely split than that of Clayton & Renvoize. The analyses of Watson & Dallwitz and Tsvelev (1976) do not closely link *Panicum* and *Echinochloa*.

Echinochloa colona (L.) Link, jungle-rice, $n = 18, 27, 28, 2n = 36, 54$, is a circumtropical annual weed and fodder crop that has become naturalized in the Southeast (Florida to Virginia, Arkansas, Tennessee, and Texas). Its awnless, small, 4-ranked spikelets are distinctive.

Echinochloa crusgalli (L.) Beauv., barnyard grass, $n = 27, 35, 36, 2n = 48, 54$,¹⁰ is a common ruderal and weed native to Eurasia. In North America it has often been confused with the native *E. muricata* (Beauv.) Fern., which has sometimes been considered conspecific with *E. crusgalli*. However, in *E. crusgalli* the dorsal surface of the distal lemma is conspicuously demarcated into a lustrous body and a green, often wrinkled apex (vs. a gradual transition from lustrous body to green apex in *E. muricata*). The demarcation zone in *E. crusgalli* has a row of minute spicules that are lacking in *E. muricata*. There is also a tendency for the spikelet hairs of *E. crusgalli* to be finer and less distinctly bulbous-based than those of *E. muricata*. Otherwise, both species are extremely variable in stature, awn length, and dimensions of the inflorescence. Three varieties of *E. crusgalli* can be recognized in the Southeast. The ruderal form most frequently encountered is var. *crusgalli*. A second, highly specialized form is var. *oryzicola* (Vasing.) Ohwi, an obligate weed of cultivated rice fields (*Oryza sativa* L.) and a native of Asia. It has hairy leaf sheaths and broadly ovate or ellipsoid distal lemmas and lacks the anthocyanic pigmentation and conspicuous leaf midrib of var. *crusgalli* (Barrett; Gould *et al.*; Yabuno, 1961). A cultivated form, var. *frumentacea* (Link) W. F. Wight (var. *edulis* Hitchc.), Japanese millet, million-dollar grass, also escapes occasionally. It lacks awns and has large fruits; also, its inflorescence and infructescence are compact (branches are closely packed and densely fruited). There is still considerable confusion about the placement of var. *frumentacea*. Clayton & Renvoize, Webster (1987), and Yabuno (1962b, 1966) believe that it is a derivative of *E. colona*. However, Barrett & Wilson (1981) and Gould *et al.* consider it to have arisen from *E. crusgalli*. Webster (1987, 1988) and Yabuno (1962b, 1966) believe that two cultivated species can be distinguished, one of which

¹⁰Maun & Barrett suggest that early reports of the chromosome number $2n = 36$ are probably incorrect. All recent counts are $2n = 54$.

is derived from *E. colona* and the other from *E. crusgalli*. If they are correct, *E. utilis* Ohwi & Yabuno is the *E. crusgalli* derivative. However, the two cultivated taxa can be distinguished only on the basis of caryopsis color, with *E. utilis* also tending to produce larger spikelets and longer primary branches. Given the degree of variability exhibited by the plants in this genus, it seems imprudent to recognize two taxa here until more evidence on the question of origins is available.

Echinochloa muricata (*E. pungens* (Poir.) Rydb.) also consists of two varieties, both of which occur in the Southeast, viz., var. *muricata* and var. *microstachya* Wieg. The latter has been treated as a distinct species by some authors (e.g., McNeill & Dore). However, there is sufficient overlap in morphology, distribution, and ecology between them to support their being treated as infraspecific taxa within *E. muricata* (Wiegand; Gould *et al.*). Variety *microstachya* is distinguished from var. *muricata* by its smaller spikelets (less than 3.5 mm long, excluding awns) and smaller anthers (less than 0.6 mm long). Clewell wondered whether *E. muricata* was really distinct from *E. crusgalli*, and Shinnery (1954) considered it to be a subspecies of the latter, while Radford *et al.* submerged it entirely.

Echinochloa cruspavonis (Kunth) Schultes, $n = 18$, $2n = 36$, 54 , is also similar to *E. crusgalli*, but it generally has ramified primary inflorescence branches, inconspicuously hairy spikelets, and short hairs on the lower panicle branches (rather than hairs as long as the spikelets). Two varieties have been recognized in North America (Gould, 1971, 1975; Gould *et al.*; Shinnery, 1954). Both are rare in the Southeast, with var. *cruspavonis* known from Florida, Mississippi, and Louisiana, and var. *macera* (Wieg.) Gould from only Louisiana. Both varieties are more widespread westward, var. *cruspavonis* in Texas and with numerous stations in western California, and var. *macera* from Kansas and Texas to California (Gould *et al.*). The typical variety differs from var. *macera* in its well-developed proximal paleas, which are at least half as long as the proximal lemmas (vs. vestigial or much less than half as long in var. *macera*), and in its long, slender, curved or drooping inflorescence axes (vs. short, stout, and erect in var. *macera*). *Echinochloa cruspavonis* has been combined with, or at least closely aligned with *E. crusgalli* by various authors (e.g., Shinnery, 1954, as *E. crusgalli* subsp. *zelayensis* (Kunth) Shinnery).

Echinochloa paludigena Wieg. occurs in wetlands in central and southern Florida, and in Bermuda and the West Indies. There is an unverified report from coastal Texas (Gould *et al.*). It differs from the other species in our area in having anthers of the staminate proximal floret 1.2 mm or more long. Wunderlin commented that it might not be distinct from *E. crusgalli*.

Echinochloa Walteri (Pursh) Heller is a robust, long-awned native annual confined largely to the Coastal Plain of eastern and southern North America, although it occurs on floodplains of major rivers in the Midwest. It is distinguished from *E. cruspavonis* (thought by Gould *et al.* to be its closest relative) and the other species in the Southeast in

its larger distal lemmas, longer awns, and coarse, bulbous-based hairs of the leaf sheaths.

Echinochloa polystachya (Kunth) Hitchc. is the only perennial species found in the Southeast (in our region known only from southern Louisiana; MacRoberts). The bulk of its range is to the south from the West Indies and Central America to central South America. It has a well-developed ligule of stiff hairs, unlike our other species.

Echinochloa crusgalli and *E. colona* have different genomic compositions, as determined from chromosome pairing relationships in hybrids. Both species are hexaploids. Yabuno (1973) suggested that *E. oryzicola* (= *E. crusgalli* var. *oryzicola*), which is tetraploid, might be the progenitor of *E. crusgalli* (var. *crusgalli*). He concluded that *E. haploclada* (also a tetraploid) was probably not the progenitor of *E. colona*, however. *Echinochloa haploclada* exhibits similar degrees of chromosome pairing in F_1 hybrids with *E. crusgalli*, *E. colona*, and *E. oryzicola*. This evidence, as well as the occurrence of diploid strains of both *E. haploclada* and *E. pyramidalis* in East Africa, suggest that tropical East Africa may be the center of origin for the genus (Yabuno, 1973).

One case of aneuploidy in *Echinochloa crusgalli* var. *crusgalli* has been reported from India (a plant with $n = 25$ ($4x-2$)). It exhibited regular meiotic behavior.

Echinochloa crusgalli is self-compatible and highly autogamous (Barrett; Maun & Barrett). Occasional apomixis has been reported in *E. frumentacea* (= *E. crusgalli* var. *frumentacea*) (Brown, 1958b). Brown (1958b) noted that apomicts among the panicoids are almost exclusively polyploid and perennial. Thus, *E. crusgalli* var. *frumentacea* is an exception to the rule, because, although it is polyploid, it is an annual.

Many species of *Echinochloa* produce diaspores that are more or less covered with stout hairs that presumably facilitate dispersal by adhesion. Davidse (1987) has noted that *E. callopus* (Pilger) Clayton and *E. pithopus* Clayton have swollen pedicels that may be elaiosomes and therefore mediate in ant dispersal. There is, as yet, no experimental evidence bearing on this observation. He also suggested that hairs on the spikelets of aquatic or semi-aquatic species might trap air, allowing for prolonged periods of buoyancy. This is known not to be the case in the heavy-seeded *E. crusgalli* var. *oryzicola* (Barrett & Wilson, 1983), but it may be true in lighter-seeded species.

Various species of *Echinochloa* have been the focus of ecological and physiological investigations. Of particular interest has been the behavior of the rice-mimic *E. crusgalli* var. *oryzicola* (Barrett & Wilson, 1981, 1983). The mimic is more similar to rice in many attributes than to its conspecific relatives (Barrett). All varieties exhibit developmental plasticity in resource allocation patterns and phenology in response to varying light and nutrient regimes, but the nature of the response differs among the taxa. In *E. crusgalli* vars. *crusgalli* and *oryzicola*, as well as in *E. muricata*, long day-length delays flowering and diverts

resources into vegetative biomass. Moreover, nutrient stress inhibits the production of secondary tillers. These effects are not seen in *E. crusgalli* var. *frumentacea*. In all experimental regimes *E. crusgalli* var. *crusgalli* flowered earlier and produced more seed than did var. *oryzicola*; vars. *frumentacea* and *E. muricata* exhibited intermediate flowering behavior and reproductive output. The failure of *E. muricata* and *E. crusgalli* var. *oryzicola* to colonize seasonally moist habitats in California may be due to an inability to reach reproductive maturity prior to the onset of drought conditions (Barrett & Wilson, 1981). Differences between *E. crusgalli* vars. *crusgalli* and *oryzicola* are also evident in seed characteristics, with the latter producing seeds that are much heavier and less buoyant than in the former. *Echinochloa crusgalli* var. *oryzicola* exhibited greater levels of seedling emergence under saturated conditions as well, which may explain why this variety increased in abundance in California rice fields following the introduction of permanent flooding as a weed control measure (Barrett & Wilson, 1983). In comparison with rice, seeds of the rice-mimic are capable of germinating at a faster rate and tolerating high levels of ethanol accumulation. The seedlings of the mimic are capable of elongating under anoxic conditions, thus enhancing its success as a weed of cultivated rice (Rumpho & Kennedy; VanderZee & Kennedy). Anoxia inhibits chlorophyll production, but exposure to oxygen and light activates its synthesis (Wang).

Echinochloa crusgalli var. *crusgalli* has also been the subject of investigations into acclimation in different environments. An ability of certain genotypes to acclimate to cool or to warm conditions explains the success of this weed at latitudes between 53°N and 40°S (Maun & Barrett). Potvin and her co-workers studied the growth responses of plants originating from different parts of North America (Quebec, North Carolina, Mississippi). All populations increased net photosynthesis and dark respiration when carbon dioxide levels or temperatures were increased under controlled conditions (Potvin & Strain, 1985a). However, in transplant experiments, plants from warm areas failed to flower in cool areas, and plants from cool areas did not survive in warm areas (Potvin). Southern populations are most susceptible to cold stress, and under certain conditions, translocation of photosynthates may be completely inhibited (Potvin *et al.*). PEP-carboxylase activity does not appear to be limiting under the experimental thermoperiod and carbon dioxide regimes, but it may become rate-limiting under environmental conditions yet to be studied (Simon *et al.*). At least under experimental conditions, plants with a shorter life cycle (those from Quebec) have more efficient translocation systems (Potvin *et al.*).

An enigmatic report of the rust *Puccinia graminis* Pers. on *Echinochloa*, known otherwise only on pooid grasses, has recently been corrected. Although an inflorescence of *E. muricata* is on the documenting herbarium sheet, the infected foliage (not connected to the

inflorescence) belongs to a pooid, *Elymus* L. (Savile, 1981). *Echinochloa polystachya* is a host for two viruses of crops: maize dwarf mosaic virus (two strains) and sugarcane mosaic virus (Rosenkranz).

The importance of some species of *Echinochloa* as weeds has already been noted. The specialized nature of *E. crusgalli* var. *oryzicola* as an obligate weed of rice fields has resulted from intensive selection for morphological and phenological characteristics that allow it to escape from weeding. Populations of this weed exist in both primitive and mechanized rice operations (Barrett). A few species of *Echinochloa* have been domesticated, including *E. crusgalli* var. *frumentacea* and *E. utilis*. *Echinochloa colona* has been cultivated in India for use as a cereal grain. It is capable of growing on poor soils, and some cultivars mature in less than two months. Four morphological races exist, but these have no geographical, ecological, or ethnological integrity (De Wet *et al.*). Several species are also either grown or collected from the field for use in seed mixtures for bird feeders. These include *E. colona*, *E. crusgalli*, *E. frumentacea* (= *E. crusgalli* var. *frumentacea*), and *E. utilis* (Hanson & Mason). A search for hydrocarbon sources among grasses by Buchanan *et al.* indicated that panicoids, including *E. crusgalli* and *E. Walteri*, generally have very low levels of such compounds.

Echinochloa crusgallis has been used as a remedy for seasickness in northwestern Venezuela and is grazed by livestock (Morton).

REFERENCES:

- Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; BROWN (1958b); BUCHANAN *et al.*; BUTZIN (1970); CHASE (1911); CHIPPIEDALL; CLAYTON (1980); CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1971, 1975, 1979); HANSON & MASON; HUGHES; MACROBERTS; MCNEILL & DORE; MORTON; OHWI; PLATZER; POHL (1980); RADFORD *et al.*; ROSENKRANZ; SHINNERS (1954); E. SMITH; TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.
- ASSÉMAT, L., H. MORISHIMA, & H. I. OKA. Neighbor effects between rice (*Oryza sativa* L.) and barnyardgrass (*Echinochloa crus-galli* Beauv.) strains. II. Some experiments on the mechanisms of interaction between plants. *Acta Oecol./Oecol. Pl.* **2**: 63-78. 1981.
- & H. I. OKA. Neighbor effects between rice (*Oryza sativa* L.) and barnyard grass (*Echinochloa crus-galli* Beauv.) strains. *Ibid.* **1**: 371-393. 1980.
- BARRETT, S. C. H. Crop mimicry in weeds. *Econ. Bot.* **37**: 255-282. 1983. [Lengthy discussion of the rice mimic, *E. crusgalli* var. *oryzicola*.]
- & B. F. WILSON. Colonizing ability in the *Echinochloa crus-galli* complex (barnyard grass). I. Variation in life history. *Canad. Jour. Bot.* **59**: 1844-1860. 1981; II. Seed biology. *Ibid.* **61**: 556-562. 1983.
- BHANWRA, R. K., & S. P. CHODA. Comparative embryology of *Echinochloa colona* and *Echinochloa crusgalli* (Poaceae). *Proc. Indian Acad. Sci. Pl. Sci.* **96**: 71-78. 1986.
- BHOWMIK, P. C., & K. N. REDDY. Effects of barnyardgrass (*Echinochloa crusgalli*) on growth, yield and nutrient status of transplanted tomato (*Lycopersicon esculentum*). *Weed Sci.* **36**: 775-778. 1988.
- BIR, S. S., & M. SIDHU. In: IOPB chromosome number reports. LX. *Taxon* **27**: 223-231. 1978. [*E. colona*, *n* = 28.]

- BROD, G. Untersuchungen zur Biologie und Ökologie der Hühnerhirse *Echinochloa crus-galli* L. Beauv. Weed Res. 8: 115-127. 1968. [Germination stimulated by high soil temperatures after cold period; light also induces germination; growth best on fertile soils with rich supply of nitrogen and ample moisture.]
- CARRETARO, J. L. El género *Echinochloa* Beauv. en el suroeste de Europa. Anal. Jard. Bot. Madrid 38: 91-108. 1981. [Five spp.]
- CRAMPTON, B. *Echinochloa oryzicola* in California. Madroño 17: 294, 295. 1964.
- DE WET, J. M. J., K. E. P. RAO, M. H. MENGESHA, & D. E. BRINK. Domestication of sawa millet (*Echinochloa colona*). Econ. Bot. 37: 283-291. 1983.
- FAIRBROTHERS, D. E. Nomenclatural change in the grass genus *Echinochloa*. Rhodora 58: 48, 49. 1956. [*E. muricata* has priority over *E. pungens*.]
- FASSETT, N. C. Some notes on *Echinochloa*. Rhodora 51: 1-3. 1949. [Notes the usefulness of the lemma apex in distinguishing among species.]
- FERNALD, M. L. Michaux's *Panicum muricatum*. Rhodora 17: 105-107. 1915. [*E. muricata* (Michx.) Fern., comb. nov.]
- GOULD, F. W., M. A. ALI, & D. E. FAIRBROTHERS. A revision of *Echinochloa* in the United States. Am. Midl. Nat. 87: 36-59. 1972. [Seven spp.; the most useful monograph for North American taxa.]
- HITCHCOCK, A. S. The North American species of *Echinochloa*. Contr. U.S. Natl. Herb. 22: 133-153. 1920. [Seven spp.]
- KENNEDY, R. A., S. C. H. BARRETT, D. VANDERZEE, & M. E. RUMPHO. Germination and seedling growth under anaerobic conditions in *Echinochloa crus-galli* (barnyard grass). Pl. Cell Environm. 3: 243-248. 1980.
- LÖVE, Á., & D. LÖVE. In: Chromosome number reports. LXX. Taxon 30: 68-80. 1981. [*E. pungens* (= *E. muricata*), $2n = 48$.]
- MALIK, C. P., & I. S. GROVER. A high polyploid *Echinochloa*. Broteria 41: 59-61. 1972. [*E. crusgalli* var. *brevisetia*; $2n = 90$.]
- MAUN, M. A., & S. C. H. BARRETT. The biology of Canadian weeds. 77. *Echinochloa crus-galli* (L.) Beauv. Canad. Jour. Pl. Sci. 66: 739-759. 1986.
- MICHAEL, P. W. A new perennial species of *Echinochloa* from New Guinea. Telopea 2: 31-33. 1980. [A perennial member of the *E. stagnina* complex.]
- & J. W. VICKERY. Two new species and a new combination in *Echinochloa*. Ibid. 1: 44-48. 1975. [Detailed descriptions, but no additional discussion.]
- & ———. Three new annual species of *Echinochloa* from northern Australia. Ibid. 2: 25-29. 1980. [Included previously within *E. stagnina*.]
- MULLIGAN, G. A. Chromosome numbers of Canadian weeds. III. Canad. Jour. Bot. 39: 1057-1066. 1961. [*E. crusgalli*, $2n = 54$.]
- MUNIYAMMA, M. Variations in microsporogenesis and the development of embryo sacs in *Echinochloa stagnina* (Retz.) P. Beauv. (Gramineae). Bot. Gaz. 139: 87-94. 1978. [Apospory in some cytotypes despite low seed set.]
- NAKAO, S., & T. YABUNO. Cytological and ecological studies on Japanese barnyard millet [*Echinochloa frumentacea* (Roxb.) Link] and its wild relatives. I. Classification of Japanese indigenous species in relation to cytology and ecology. Seiken Zihô 5: 58-64. 1952. [Five taxa discussed.]
- NARAYANASWAMI, S. The structure and development of the caryopsis in some Indian millets. IV. *Echinochloa frumentacea* Link. Phytomorphology 5: 161-171. 1955.
- PONS, T. L. Factors affecting weed seed germination and seedling growth in lowland rice in Indonesia. Weed Res. 22: 155-161. 1982. [Seeds of *E. colona* and *E. crusgalli* germinated on the soil surface of both aerobic and anaerobic soils, but only germinated in aerobic soils when buried.]
- POTVIN, C. Biomass allocation and phenological differences among southern and northern populations of the C_4 grass *Echinochloa crus-galli*. Jour. Ecol. 74: 915-923. 1986.

- , J. D. GOESCHL, & B. R. STRAIN. Effects of temperature and CO₂ enrichment on carbon translocation of plants of the C₄ grass species *Echinochloa crus-galli* (L.) Beauv. from cool and warm environments. *Pl. Physiol.* **75**: 1054–1057. 1984.
- & B. R. STRAIN. Photosynthetic response to growth temperature and CO₂ enrichment in two species of C₄ grasses. *Canad. Jour. Bot.* **63**: 483–487. 1985a. [*Echinochloa crus-galli*, *Eleusine indica* (L.) Gaertner.]
- & ———. Effects of CO₂ enrichment and temperature on growth in two C₄ weeds, *Echinochloa crus-galli* and *Eleusine indica*. *Ibid.* 1495–1499. 1985b.
- , ——— & J. D. GOESCHL. Low night temperature effect on photosynthate translocation of two C₄ grasses. *Oecologia* **67**: 305–309. 1985.
- ROCHÉ, B. F., & T. J. MUZIK. Ecological and physiological study of *Echinochloa crus-galli* (L.) Beauv. and the response of its biotypes to sodium 2,2-dichloropropionate. *Agron. Jour.* **56**: 155–160. 1964. [Different strains vary in their susceptibility to this herbicide; some discussion of intra-plant variation in seed color and weight.]
- RUMPHO, M. E., & R. A. KENNEDY. Anaerobic metabolism in germinating seeds of *Echinochloa crus-galli* (barnyard grass). *Pl. Physiol.* **68**: 165–168. 1981.
- SÁNCHEZ, E. Anatomía foliar de las especies del género *Echinochloa* (Gramineae) de la flora Argentina. *Bol. Soc. Argent. Bot.* **12**: 17–37. 1968. [Leaf anatomy of nine taxa described, illustrated; key.]
- SAVILE, D. B. O. The supposed rust of *Echinochloa*. *Mycologia* **73**: 1007, 1008. 1981.
- SIMON, J.-P., C. POTVIN, & B. R. STRAIN. Effects of temperature and CO₂ enrichment on kinetic properties of phospho-enol-pyruvate carboxylase in two ecotypes of *Echinochloa crus-galli* (L.) Beauv., a C₄ weed grass species. *Oecologia* **63**: 145–152. 1984.
- SUNG, S.-J. S., G. R. LEATHER, & M. G. HALE. Development and germination of barnyardgrass (*Echinochloa crus-galli*) seeds. *Weed Sci.* **35**: 211–215. 1987.
- VANDERZEE, D., & R. A. KENNEDY. Germination and seedling growth in *Echinochloa crus-galli* var. *oryzicola* under anoxic conditions: structural aspects. *Am. Jour. Bot.* **68**: 1269–1277. 1981.
- WANG, W.-Y. Photoactivation of chlorophyll synthesis and cytochrome oxidase activity in anaerobically germinated seedlings of *Echinochloa crus-galli* var. *oryzicola*. *Pl. Physiol.* **65**: 451–454. 1980.
- WIEGAND, K. M. The genus *Echinochloa* in North America. *Rhodora* **23**: 49–65. 1921. [Revision; twelve spp. and numerous vars.; incl. *E. paludigena* Wieg., sp. nov.]
- YABUNO, T. Morphological and cytological studies in the genus *Echinochloa*. *Seiken Zihô* **6**: 66–71. 1953. [Chromosome numbers, inflorescence morphology of five taxa and hybrids.]
- . *Oryza sativa* and *Echinochloa crus-galli* var. *oryzicola* Ohwi. *Ibid.* **12**: 29–34. 1961. [Cytology, morphology, and ecology of the rice mimic.]
- . A hybrid between the tetraploid annual *Echinochloa crus-galli* var. *oryzicola* and 60-1, a tetraploid perennial strain from West Bengal. *Ibid.* **13**: 52–56. 1962a.
- . Cytotaxonomic studies on the two cultivated species and the wild relatives in the genus *Echinochloa*. *Cytologia* **27**: 296–305. 1962b. [Hypothesizes that *E. frumentacea* arose from *E. colona*, and *E. utilis* arose from *E. crus-galli*.]
- . Biosystematic study of the genus *Echinochloa*. *Jap. Jour. Bot.* **19**: 277–323. 1966. [Cytogenetic, morphological, and ecological data on eight taxa from around the world.]
- . Biosystematic studies of *Echinochloa stagnina* (Retz.) P. Beauv. and *E. pyramidalis* (Lamk.) Hitchc. et Chase. *Cytologia* **33**: 508–519. 1968.
- . Biosystematics of *Echinochloa stagnina* (Retz.) P. Beauv., cytological relationship between the 12- and 14-ploid strains. *Genetica* **41**: 311–315. 1970.

[Meiosis normal in both strains, but desynapsis prevalent in the hybrid; the strains only distantly related and should be considered distinct species.]

———. Cytological relationships between some *Echinochloa* species and Kenyan *E. haploclada* (Stapf) Stapf. *Cytologia* **38**: 131–135. 1973.

———. A biosystematic study on *Echinochloa oryzoides* (Ard.) Fritsch. *Ibid.* **49**: 673–678. 1984. [Hybrids easily produced with varieties of *E. crusgalli*.]

13. **Alloteropsis** J. S. Presl in C. B. Presl, *Rel. Haenk.* **1**: 343. 1830, emend. Hitchcock, *Contr. U.S. Natl. Herb.* **12**: 210. 1909.

Caespitose or decumbent annuals [perennials]. Stems from tuberous or non-tuberous bases; internodes hollow; nodes glabrous or pubescent. Leaves mostly on lower part of stem; sheaths pubescent; ligule a fringe of hairs with small basal membrane; blades linear to lanceolate, glabrous [pubescent] above, pubescent below, flat or folded, truncate or rounded at base, rolled in bud; photosynthesis C_3 and C_4 , with PCK and NADP-me biochemical pathways. Inflorescences of [2] 4–7 spike-like primary branches, digitate or not, secondary branches appressed and terminating in spikelets. Spikelets ovate [lanceolate], dorsiventrally compressed, disarticulating below the glumes, abaxial, secund, short-pedicellate (pedicel apices cupuliform), solitary or in small clusters of two or three at the ends of branches; proximal florets staminate, paleate or epaleate; rachilla pronounced between florets. Calli undifferentiated. Glumes 2, chartaceous; proximal glumes awned, 1–3 nerved, shorter than ciliate, 3–7 nerved distal glumes. Proximal lemmas chartaceous, with basal hyaline region; distal lemmas chartaceous to cartilaginous, striate to muricate, glabrous [with small clavate hairs near margins], brown to yellow, dull, awned, with flat or involute margins and conspicuous germination flap. Distal paleas awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red. Caryopses (grains) smooth; endosperm hard, containing only simple starch grains. Base chromosome number 9. (Including *Coridochloa* Nees.) TYPE SPECIES: *Alloteropsis distachya* J. S. Presl = *A. semialata* (R. Br.) Hitchc., the only species included in the genus at the time of its original description. (Name from Greek, *allotrios*, exotic, and *opsis*, like.) -- BUGSEED GRASS.

A genus of five species native to Old World tropical grasslands and marshes, with one species, *A. cimicina* (L.) Stapf, bugseed grass, naturalized in Florida on open shores of lakes and in grasslands, cultivated fields, and disturbed ground. The diagnostic features of *Alloteropsis* include awned proximal glumes, ciliate distal glumes, staminate proximal florets, hyaline basal areas on the proximal lemmas, awned distal lemmas, and elongated rachillas between the florets (Webster, 1988).

Polyploidy is established in the genus. *Alloteropsis cimicina* contains diploids and tetraploids, *A. cf. Homblei* Robyns is diploid, and *A. semialata* contains diploids and hexaploids (Chen & Hsu, 1962; De Wet, 1958; Hoshino & Davidse; Moffett & Hurcombe; Tateoka, 1965b).

Webster (1988) suggested two possible directions of relationship for *Alloteropsis*. These depend upon what characters are most heavily weighted. Features of the distal floret suggest a relationship to *Digitaria*, while inter-floret rachilla elongation and other characters suggest a relationship with *Eriochloa* Kunth and *Urochloa* Beauv. Clayton & Renvoize believe that *Alloteropsis* is probably derived from *Panicum*. An analysis of phenetic similarity suggests that *Eriochloa* and *Brachiaria* (= *Urochloa* for the most part) are most similar to *Alloteropsis* (Watson & Dallwitz).

Alloteropsis semialata is the only known grass with both C_3 and C_4 photosynthetic pathways. Anatomical modifications are correlated with this physiological diversity. Gibbs Russell (1983) claimed that morphological features such as leaf-blade tip-width and basal leaf-sheath vein-width differed between the photosynthetic types, and she recognized each type as a distinct subspecies. However, she acknowledged that the geographical ranges of the two subspecies overlap in southern Africa and that intermediate forms existed in central Africa. Frean *et al.* (1983) found no consistent correlations between morphology and photosynthetic type. They also found variation in chloroplast morphology in bundle-sheath and mesophyll cells that is related to the ontogenetic stage of leaf or sheath, light regime, and photosynthetic type. Most recently, however, Frean & Marks (1988) noted a correlation between ploidy and photosynthetic type. Plants of the C_3 type were diploid ($2n = 18$), and C_4 plants were allohexaploids ($2n = 54$), with regular bivalent formation. They concluded that the two types should be recognized as separate species. Undoubtedly, the C_3 condition is primitive, and most likely the C_4 condition has evolved several times within tribe Paniceae.

Alloteropsis semialata is also unique among C_4 grasses in having PEP-carboxykinase activity and a double bundle sheath in which the outer sheath consists of small cells with few or no chloroplasts (the specialized photosynthetic plastids are in the inner sheath cells), rather than the densely chlorophyllose outer sheath normally associated with this biochemical type (Ellis, 1974a; Prendergast *et al.*). *Alloteropsis cimicina* has the more usual double sheath (Prendergast & Hattersley).

REFERENCES:

Under references for tribe see BOLKHOVSKIKH *et al.*; CHASE (1911); CHIPFINDALL; CLAYTON & RENVOIZE; DE WET (1958); HITCHCOCK (1909); HOSHINO & DAVIDSE; HUGHES; MOFFETT & HURCOMBE; PRENDERGAST & HATTERSLEY; PRENDERGAST *et al.*; TATEOKA (1965b); WATSON & DALLWITZ; and WEBSTER (1987, 1988).

BARRETT, D. R., M. L. FREAN, & C. F. CRESSWELL. C_3 and C_4 photosynthetic and anatomical forms of *Alloteropsis semialata* (R. Br.) Hitchcock. 1. Variability in photosynthetic characteristics, water utilization efficiency and leaf anatomy. *Ann. Bot.* II. 51: 801–809. 1983.

BUTZIN, F. Bemerkungen zum Umfang und zur Morphologie der Paniceengattung *Alloteropsis*. *Willdenowia* 5: 123–143. 1968. [Infrageneric classification; comments on related genera.]

- CHEN, C.-C., & C.-C. HSU. Cytological studies on Taiwan grasses (2). Chromosome numbers of some miscellaneous tribes. Jour. Jap. Bot. **37**: 300-313. 1962. [*A. semialata*, $n = 9$.]
- ELLIS, R. P. Anomalous vascular bundle sheath structure in *Alloteropsis semialata* leaf blades. Bothalia **11**: 273-275. 1974a.
- . The significance of the occurrence of both kranz and non-kranz leaf anatomy in the grass species *Alloteropsis semialata*. S. Afr. Jour. Sci. **70**: 169-173. 1974b.
- FREAN, M. L., D. ARIOVICH, & C. F. CRESSWELL. C₃ and C₄ photosynthetic and anatomical forms of *Alloteropsis semialata* (R. Br.) Hitchcock. 2. A comparative investigation of leaf ultrastructure and distribution of chlorenchyma in the two forms. Ann. Bot. II. **51**: 811-821. 1983.
- , D. R. BARRETT, D. ARIOVICH, M. WOLFSON, & C. F. CRESSWELL. Intraspecific variability in *Alloteropsis semialata* (R. Br.) Hitchc. Bothalia **14**: 901-913. 1983. [No consistent morphological features correlate with photosynthetic types.]
- & E. MARKS. Chromosome numbers of C₃ and C₄ variants within the species *Alloteropsis semialata* (R. Br.) Hitchc. (Poaceae). Bot. Jour. Linn. Soc. **97**: 255-259. 1988. [Photosynthetic types seem to correspond to different ploidy levels and therefore the two forms should be recognized as species.]
- GIBBS RUSSELL, G. E. The taxonomic position of C₃ and C₄ *Alloteropsis semialata* (Poaceae) in southern Africa. Bothalia **14**: 205-213. 1983. [Two forms recognized as subspecies; necessary combination made.]
- WOLFSON, M. M., & C. F. CRESSWELL. An investigation into the activity of the photosynthetic pathway enzymes in *Alloteropsis semialata*. (Abstr.) S. Afr. Jour. Bot. **1**: 83. 1982.

14. *Urochloa* Palisot de Beauvois, Essai Agrost. 52. 1812.

Rhizomatous, stoloniferous, decumbent or caespitose perennials or annuals. Stems from tuberous or non-tuberous bases, branched or unbranched above; internodes solid or hollow; nodes glabrous to pubescent. Leaves with sheaths glabrous to pubescent; ligule a fringed membrane [fringe of hairs]; blades linear to lanceolate, flat (folded) [falcately recurved], glabrous to pubescent, rolled in bud, margins sometimes cartilaginous and spinulose, bases cuneate to truncate; photosynthesis C₄, biochemical pathway PEP-ck. Inflorescences paniculate, primary branches 2-23, digitate or racemose, spike-like; secondary branches appressed to spreading, terminating in spikelets [points]. Spikelets dorsiventrally compressed, planoconvex, disarticulating below the glumes, abaxial or adaxial, secund or not, subsessile or pedicellate (pedicel apices oblique, cupuliform or discoid), solitary or paired, biseriate, rachilla sometimes slightly elongated between glumes; proximal florets staminate or sterile, paleate or epaleate. Calli undifferentiated or prolonged. Glumes 2, equal or unequal, glabrous or pubescent, awnless; proximal glumes membranaceous, acute to truncate, 0-5 nerved, encircling spikelet base; distal glumes equalling proximal lemmas, membranaceous, acute to mucronate, 5-9 [11] nerved. Proximal lemmas equalling or exceeding distal lemmas, sometimes grooved, acute to mucronate, awnless, 5-11 nerved; distal lemmas cartilaginous, rugose, glabrous, obtuse to acute or mucronate, awnless [awned], with involute margins and a

conspicuous germination flap. Distal paleas rugose, entire, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red. Caryopses (grains) small, smooth; pericarp thin; endosperm hard, without lipid, containing only simple starch grains. Base chromosome numbers 6, 7, 8, 9, 10, 13. (Including *Brachiaria* (Trin.) Griseb. pro parte, *Leucophrys* Rendle, *Pseudobrachiaria* Launert.) TYPE SPECIES: *Urochloa panicoides* Beauv., the only species included in the genus at the time of its original description. (Name from Greek, *uro-*, tailed or appendaged, and *chloa*, grass, in reference to the mucronate or short-awned spikelets of some species.) — PARAGRASS, SIGNALGRASS.

A genus of about 110 species occurring in tropical and subtropical regions of the world. The most frequent habitats include moist or dry grasslands, stream banks, pastures, cultivated ground, and disturbed areas. The greatest diversity of species is found in the Old World tropics. Webster (1987, 1988) has radically altered the traditional views of *Urochloa* and *Brachiaria* (Trin.) Griseb., but his treatment of generic limits is more sensible than those of previous authors. He considers all species formerly placed in *Brachiaria*, with the exception of *B. eruciformis* (Sm.) Griseb.,¹¹ the type species, to be members of *Urochloa*. All of them differ from *B. eruciformis* in having rugose distal floret bracts. Species included in groups "Fasciculata" and "Maxima" of *Panicum* (Hitchcock & Chase, 1910) also have rugose distal lemmas and paleas, and they have been transferred to *Urochloa* (Webster, 1987). These realignments make the three genera more natural assemblages.

Spikelet orientation had been used to distinguish between *Brachiaria* and *Urochloa* in previous classification schemes, but Clayton & Renvoize, Webster (1987, 1988), and others have realized that this feature is difficult to interpret, or variable when spikelets are paired. Its usefulness in these genera is limited. Webster (1987, 1988) also based his circumscription of *Urochloa* on the fact that many species of *Brachiaria* were more similar to species of *Urochloa* than to *B. eruciformis*. Clayton & Renvoize noted that no satisfactory infrageneric classification exists for *Brachiaria* in the broad sense, and of course, this holds true for the expanded *Urochloa*.¹²

Urochloa is most closely related to the other genera with rugose distal floret bracts, such as *Eriochloa*, *Setaria*, and *Paspalidium* (Pohl, 1980; Clayton & Renvoize; Thompson & Estes; Webster, 1987, 1988). The phenetic analysis of Watson & Dallwitz supports this, and adds *Arthrargrostis* as a genus similar to *Brachiaria sensu lato*. In their

¹¹*Brachiaria eruciformis* (Sm.) Griseb., $n = 9, 18$ (Basappa & Muniyamma; Malik & Mary; Mehra & Sharma, 1975; Sarkar *et al.*, 1980; Sharma & Kaur) has been cultivated in Florida, but it is not known to have become naturalized (Hall; Webster, 1988).

¹²Stapf (1919–1934) provided names for subdivisions within *Brachiaria* in Africa, but these were not described and are therefore informal groupings similar to those used by Hitchcock & Chase (1910) in *Panicum*.

analysis *Panicum*, *Yakirra*, *Tricholaena* (subtribe Melinidinae) and *Brachiaria* are most similar to *Leucophrys* Rendle (a segregate of *Urochloa*), and *Paspalum* (along with *Eriochloa*, *Paspalidium*, and *Setaria*) is very similar to *Urochloa*. However, *Urochloa* utilizes the PEP-carboxykinase acid decarboxylation pathway, and in this way, differs from these genera, except *Eriochloa* (Brown, 1977; Gutierrez *et al.*; Hattersley, 1984; Prendergast & Hattersley). Butzin (1970) placed *Urochloa* in subtribe Brachiariinae with *Axonopus*, *Eriochloa*, and *Reimaria* Flügge (= *Reimarochloa*, in part). However, this arrangement does not agree with other estimates of relationship, nor is there any reason to believe that it is an improvement on other classifications.

Thirteen species of *Urochloa* occur in the Southeast. All have been treated in either *Brachiaria* or *Panicum* in earlier floras and revisions. A few of the species, including *U. adspersa* (Trin.) R. Webster, *U. ciliatissima* (Buckley) R. Webster, *U. fasciculata* (Sw.) R. Webster, *U. platyphylla* (Griseb.) R. Webster, and perhaps *U. texana* (Buckley) R. Webster, are native to the region. *Urochloa adspersa* (*Panicum adspersum* Trin., *Brachiaria adspersa* (Trin.) Parodi) (annual, panicle branches scabrous, pubescent in the axils, spikelets 3.2–4 mm long, pubescent, proximal floret staminate) grows in moist, open fields and occurs in our area in Florida and Alabama. *Urochloa ciliatissima* (*Brachiaria ciliatissima* (Buckley) Chase), fringed signalgrass, $2n = 36$, (perennial, spikelets 3.5–4.5 mm long, distal glume and proximal lemma densely hairy) has been reported from northwestern Arkansas (Chase, 1920; Gould, 1975; E. Smith).¹³ *Urochloa fasciculata* (*Panicum fasciculatum* Sw., *Brachiaria fasciculata* (Sw.) S. T. Blake), $n = 9, 18$, (annual, panicle broad, with secund branches, spikelets 2.1–3 mm long, proximal floret staminate), occurs in Louisiana (MacRoberts). *Urochloa platyphylla* (*Brachiaria extensa* Chase, *B. platyphylla* (Griseb.) Nash), broadleaf signalgrass, $n = 18$, (annual, inflorescence branches winged, spikelets 3.5–4.7 mm long, proximal lemmas seven nerved, anastomosing veins of spikelet prominent) inhabits swampy woods and wet, disturbed sites from North Carolina, Kentucky, and Missouri southward throughout our area. *Urochloa texana* (*Panicum texanum* Buckl., *Brachiaria texana* (Buckl.) S. T. Blake), Texas millet, Texas panicum, $2n = 36, 54$, (annual, panicles broad, inflorescence branches pubescent, spikelets sessile, 5–6 mm long, proximal floret staminate) grows in ditches and along the edges of cultivated fields and has been found in the eastern United States from Kentucky

¹³Although consistent chromosome numbers have been reported for certain species of *Urochloa*, a number of species in the following account have widely varying numbers, without any consistency in either base number or absolute number. If these numbers are correct, then aneuploidy within species is rampant. However, the differences are sometimes so large that either the counts or the plant identifications are dubious. Therefore, the reader is cautioned against accepting chromosome counts at face value, except when the cytological system is well understood, as in the $2n = 16$ and 32 races of *U. maxima* (Jacq.) R. Webster. An examination of voucher specimens is necessary before the situation in most cases can be resolved.

and North Carolina southward to Arkansas, Texas, Louisiana, and Florida. It is with certainty native to Texas and Mexico, but more easterly populations may be adventive (Blomquist; Clewell; Wunderlin).

Several species of *Urochloa* have been introduced into the Southeast and are naturalized. *Urochloa maxima* (Jacq.) R. Webster (*Panicum maximum* Jacq.), Guinea grass, $n = 8, 16, 18, 27, 2n = 48$, (perennial, panicles broad, branches not secund, spikelets 3–3.5 mm long, proximal florets staminate), native to Africa, has escaped from cultivation and is naturalized in Florida and Georgia. *Urochloa mutica* (Forskål) Nguyen (*Panicum purpurascens* Raddi, *Brachiaria mutica* (Forskål) Stapf), para grass, $n = 18, 26$, (stoloniferous, leaves pubescent, spikelets 2.7–3 mm long, paired, proximal floret staminate) occurs at disturbed sites in South Carolina, Florida, and Alabama. *Urochloa piligera* (F. Mueller ex Benth) R. Webster (*Brachiaria piligera* (F. Mueller ex Benth) Hughes), hairy signalgrass (inflorescence branches winged, spikelets 3.8–4.3 mm long, closely overlapping, pubescent or glabrous, proximal floret sterile and lacking a palea) is a weed of disturbed sites in central Florida. *Urochloa plantaginea* (Link) R. Webster (*Brachiaria plantaginea* (Link) Hitchc.), creeping signalgrass, $n = 36, 2n = 36 + 2B$, (inflorescence branches narrowly winged, spikelets 4–5.4 mm long, glabrous, unbeaked, proximal lemmas seven nerved, anastomosing veins of spikelets obscure), a weed of roadsides in Florida, presumably originated from native populations in Central and South America. It has also appeared in ballast as far north as Philadelphia, Pennsylvania, and Camden, New Jersey (Chase, 1920). The African *Urochloa platytaenia* (Stapf) Crins¹⁴ (*Brachiaria platytaenia* Stapf) (spikelets 4.7–5.2 mm long, proximal glumes 2.8–3 mm long) has been recorded once in southern Florida, on roadside muck (Hall). *Urochloa ramosa* (L.) R. Webster (*Panicum ramosum* L., *Brachiaria ramosa* (L.) Stapf), browntop millet, $n = 7, 12, 16, 18, 21, 2n = 36, 72$, (leaves glabrous, spikelets 2.5–3.5 mm long, proximal floret sterile, distal glumes and proximal lemmas acute to acuminate, pubescent or glabrous, proximal lemmas 5 nerved) has also escaped from cultivation, and is a sparse roadside weed from southern North Carolina and Arkansas southward through Florida and Alabama. It is native to Africa and Asia. *Urochloa reptans* (L.) Stapf (*Panicum reptans* L., *Brachiaria reptans* (L.) C. A. Gardner & C. E. Hubb.), $n = 7, 9$, (inflorescence branches unwinged, spikelets 2 mm long or less, proximal glumes and proximal lemmas glabrous), a native of Asia, occurs as an adventive in Texas, Louisiana, Mississippi, Alabama, and Florida. *Urochloa subquadriflora* (Trin.) R. Webster (*Brachiaria subquadriflora* (Trin.) Hitchc.), $n = 36, 42$, (leaves glabrous or pubescent, nodes glabrous, inflorescence branches winged, spikelets 3.3–3.8 mm long, glabrous, proximal florets sterile, proximal paleas well developed) is also an Asian species that

¹⁴*Urochloa platytaenia* (Stapf) Crins, comb. nov. Based on *Brachiaria platytaenia* Stapf, Fl. Trop. Afr. 9: 524. 1919.

has escaped from cultivation and grows at disturbed sites in southern and central Florida. Several other species, e.g., *U. brizantha* (A. Rich.) R. Webster, *U. mosambicensis* (Hackel) Dandy (*U. pullulans* Stapf), have been cultivated in the Southeast but have not yet become established (Hall).

Urochloa maxima is of immense economic importance in the tropics as a forage crop, and for this reason, its morphological variation and breeding systems have been extensively investigated. On the basis of morphometric analyses using principal components analysis, three morphotypes have been recognized by Chaume. Plants from some populations are much more variable than others in multivariate space. *Urochloa maxima* was distinct from related segregates (*Panicum infestum* Anderss., *P. trichocladum* Reichenb. ex Kunth) in these analyses (Chaume; Pernès *et al.*). Jauhar & Joshi (1966) and Warmke (1951) recognized five morphotypes within this species, but it is not clear how these relate to the three morphotypes recognized by Chaume. *Urochloa maxima* (and several other species of *Urochloa*) contains tetraploid races ($2n = 32$, $2n = 36$) that are aposporous and produce 4-nucleate embryo sacs (Brown & Emery, 1957a, 1958; Jauhar & Joshi, 1966; Pohl & Davidse, 1971; Pritchard; Sotomayor-Ríos *et al.*, 1960; Warmke, 1954). Such plants are also pseudogamous (Warmke, 1954). Diploid races of these and other species in the genus produce typical 8-nucleate embryo sacs and reproduce sexually. *Urochloa maxima* has evolved a cyclic system of tetraploidization and haploidization, coupled with apomictic and sexual reproduction, which provides a means of generating morphological variability through genetic recombination of apomictic genotypes. This is accomplished by the production of tetraploids through the crossing of unreduced gametes from diploids with tetraploid gametes, a period of apomictic reproduction, and eventually, the production of dihaploids through the parthenogenetic development of diploid gametes from the apomictic tetraploids (Savidan & Pernès). At least in *U. maxima*, apomixis behaves genetically as a single gene, the allele for apomixis being dominant over that for sexuality (Savidan & Pernès; R. Smith, 1972). Artificial hybridization between apomictic and sexual plants generally leads to nearly completely apomictic progeny (Savidan).

Urochloa panicoides Beauv. also contains several true-breeding varieties in which cell division may be irregular, but seed set and pollen fertility are apparently not affected in this system (Basavaiah & Murthy).

Embryo culture has been attempted in *Urochloa maxima* to produce uniform seedlings for planting. Plantlets have been obtained from embryogenic calluses, and these have the normal somatic chromosome complement, $2n = 32$ (Lu & Vasil, 1981, 1982, 1985).

Polyploidy is fairly common in *Urochloa*. Both *U. maxima* and *U. texana* contain chromosome races. Within the genus as a whole, diploid through octoploid levels are known in different species (Bolikhovskikh *et al.*; De Wet & Anderson). In most documented cases involving tetraploidy or higher ploidy levels, chromosome pairing is

disturbed. Univalents, multivalents, laggards, and chromosome stickiness have been observed (Nath *et al.*; Pritchard; Sotomayor-Ríos *et al.*, 1970), and pollen stainability and/or seed set are lowered.

Davidse & Pohl (1974) have noted occasional multivalents in an aneuploid ($n = 18$) plant of *U. maxima* from Venezuela. A plant of this species with $n = 27$ [hexaploid based on the aneuploid (in this species) base number of 9] has been found in India (Bir & Sahni). Aneuploidy probably began long ago, since several chromosome base numbers now exist within *Urochloa*. The original base number was perhaps 9, but $x = 6, 7, 8, 10$, and 13 are also found in various species (Basappa & Muniyamma; Bir & Sahni; Bolkhovskikh *et al.*; Jauhar & Joshi, 1969; Olorode; Raman *et al.*, 1959a, b). Two reports of B chromosomes have also been made. In Costa Rican *U. plantaginea* the somatic complement of 36 chromosomes was supplemented by two B chromosomes (Pohl & Davidse, 1971). Other counts for this species are $n = 36$. In a population of *U. ramosa* five extra, entirely heterochromatic pairs of chromosomes were found at meiosis, but chromosome behavior was normal (Singh).

In South African velds species of *Urochloa* tend to be important components of the intermediate seral stages (Gibbs Russell, 1983). They decrease in abundance with either over- or under-grazing. Other species, such as *U. ruziziensis* (Germain & Evrard) Crins¹⁵ (*Brachiaria ruziziensis* Germain & Evrard) may also be dominants in grasslands and marshes in other parts of the tropics (Germain & Evrard; L. Smith).

Several species of *Urochloa* possess enlarged pedicel tips that may serve as elaiosomes that assist in the dispersal of fruits by ants (Davidse, 1987). The species of *Urochloa* also have indurate bracts surrounding the caryopsis. These might provide protection while the fruit passes through the digestive tracts of mammals or birds. The seeds of at least some species require scarification to break dormancy, and measurements of O_2 uptake suggest that the restriction of gas exchange across the seed coat may be responsible for the dormancy (Renard & Capelle).

Urochloa maxima is an extremely important forage crop in the tropics (Chaume; Morton; Sotomayor-Ríos *et al.*, 1960). Other species have been grown for this purpose as well. Ten species have been introduced into Brazil as pasture grasses (Sendulsky). In Puerto Rico *U. brizantha* (A. Rich.) R. Webster has been shown to be as palatable to livestock as Napier grass (*Pennisetum purpureum*), which is also an important tropical forage grass. The former contains more dry matter per pound of green forage than does the latter (Brenes *et al.*; Rivera-Brenes *et al.*). It also compares favorably in terms of yield, mineral content, drought resistance, and lignin content with *U. maxima* (Sotomayor-Ríos *et al.*, 1960).

¹⁵*Urochloa ruziziensis* (Germain & Evrard) Crins, comb. nov. Based on *Brachiaria ruziziensis* Germain & Evrard, Bull. Jard. Bot. État Brux. 23: 373. 1953.

In addition to their beneficial qualities several species of *Urochloa* have been implicated in causing various ailments in livestock. BOR (1960) noted that *U. brizantha* caused photosensitization and ultimately death in sheep in Asia. *Urochloa maxima* has also been known to cause dermatitis in sheep when the spikelets are infected with smut fungi (*Ustilago* L.). *Urochloa platyphylla* serves as an alternate host for two strains of maize dwarf mosaic virus and sugarcane mosaic virus (Rosenkranz).

Some species are incidental or more serious weeds. *Urochloa platyphylla* and *U. panicoides* are occasionally included in commercial bird seed mixtures, and are sometimes spontaneous under bird feeders in England (Hanson & Mason). *Urochloa platyphylla* also causes significant reductions in the yields of rice (*Oryza sativa*) when interspecific competition persists for 40 days or longer. Its own growth is also negatively affected at high densities (McGregor *et al.*, 1988a, b).

REFERENCES:

Under references for tribe see BAQUAR & SAEED; BHANWRA; BIR & SAHNI; BLAKE; BLUMQUIST; BOLKHOVSKIKH *et al.*; BOR (1960); BRENES *et al.*; BROWN (1951, 1958a, 1977); BROWN & EMERY (1957a, 1958); BROWN *et al.* (1959); BUTZIN (1970); CHASE (1911); CHIPPINDALL; CLAYTON (1980); CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); DAVIDSE & POHL (1972b, 1974); DE WET & ANDERSON; GIBBS RUSSELL (1983); GOULD (1958, 1975); GOULD & SODERSTROM (1967, 1970); GUTIERREZ *et al.*; HALL; HANSON & MASON; HATCH *et al.* (1975); HATTERSLEY (1984); HITCHCOCK & CHASE (1910); HSU (1963, 1965, 1972); HUGHES; JONES & COILE; MACROBERTS; MORTON; NATH *et al.*; OLORODE; PARODI; POHL (1980); POHL & DAVIDSE (1971); PRENDERGAST & HATTERSLEY; PRITCHARD; RADFORD *et al.*; RAMAN *et al.* (1959a, b); REEDER (1957, 1967, 1968); RIVERA-BRENES *et al.*; ROSENKRANZ; E. SMITH; STAFF (1919-1934); TSVELEV (1976); WATSON & DALLWITZ; WATSON & JOHNSTON; WEBSTER (1987, 1988); and WUNDERLIN.

BASAPPA, G. P., & M. MUNIYAMMA. In: Chromosome number reports. LXXII. Taxon 30: 694-708. 1981. [Counts for 19 species of *Brachiaria* (including *Urochloa*).]

BASAVAIAH & T. C. S. MURTHY. Cytomixis in pollen mother cells of *Urochloa panicoides* P. Beauv. (Poaceae). Cytologia 52: 69-74. 1987. [Claims that cytomixis (cytoplasmic interchange between cells during meiosis) is an expression of an unbalanced genetic system responding to environmental conditions; pollen fertility and seed set unaffected.]

BURNELL, J. N. Purification and properties of phosphoenolpyruvate carboxykinase from C₄ plants. Austral. Jour. Pl. Physiol. 13: 577-587. 1986. [*U. panicoides* and *U. maxima* examined, of the Paniceae.]

———. Photosynthesis in phosphoenolpyruvate carboxykinase-type C₄ species: properties of NAD-malic enzyme from *Urochloa panicoides*. Ibid. 14: 517-525. 1987.

CHASE, A. The North American species of *Brachiaria*. Contr. U.S. Natl. Herb. 22: 33-43. 1920. [All species treated now considered to be in *Urochloa*, except for the type species, *B. eruciformis*; six spp.]

CHAUME, R. Organisation de la variabilité génétique du complexe agamique *Panicum maximum* en vue de son utilisation en amélioration des plantes. Éditions ORSTOM, Trav. Documents No. 184. 243 pp. 1985. [= *U. maxima*.]

- DUNCAN, W. H. Preliminary reports on the flora of Georgia—4. Notes on the distribution of flowering plants including species new to the state. *Castanea* 15: 145–159. 1950. [*U. ramosa*, as *Panicum ramosum*, in Clarke Co.]
- GERMAIN, R., & C. EVRARD. Un nouveau *Brachiaria* de l'est du Congo Belge. *Bull. Jard. Bot. État Brux.* 23: 373–377. 1953. [= *U. ruziziensis*; see footnote 15.]
- GOBBE, J., B. LONGLY, & B.-P. LOUANT. Calendrier des sporogénèses et gamétogénèses femelles chez le diploïde et le tétraploïde induit de *Brachiaria ruziziensis* (Graminée). *Canad. Jour. Bot.* 60: 2032–2036. 1982. [= *U. ruziziensis*; see footnote 15.]
- JAUHAR, P. P., & A. B. JOSHI. Cytotaxonomic investigations in the *Panicum maximum* Jacq. complex. I. Morphological studies. *Bull. Bot. Surv. India* 8: 287–295. 1966. II. Studies on epidermal pattern. *Ibid.* 9: 59–62. 1967. III. Cytological features, chromosome diminution and evolution of the karyotype. *Cytologia* 34: 222–233. 1969. [= *U. maxima*; five morphotypes characterized; all $2n = 32$; “intraspecific autopolyploid” (equivalent to segmental allopolyploid?); this chromosome number evidently derived from the loss of chromosomes through unequal reciprocal translocations from an ancestor with a base number of $x = 9$, rather than from doubling of the chromosome complement of an ancestor with a base number of $x = 8$.]
- LAUNERT, E. Miscellaneous taxa of Gramineae from South West Africa and adjacent areas. *Mitt. Bot. Staatssamml. München* 8: 147–163. 1970. [Transfers *Leucophrys* to *Brachiaria*; *Pseudobrachiaria* described.]
- LU, C.-Y., & I. K. VASIL. Somatic embryogenesis and plant regeneration from freely suspended cells and cell groups of *Panicum maximum* Jacq. *Ann. Bot.* II. 48: 543–548. 1981. [= *U. maxima*.]
- & ———. Somatic embryogenesis and plant regeneration in tissue cultures of *Panicum maximum* Jacq. *Am. Jour. Bot.* 69: 77–81. 1982. [= *U. maxima*.]
- & ———. Histology of somatic embryogenesis in *Panicum maximum* (guinea grass). *Ibid.* 72: 1908–1913. 1985. [= *U. maxima*.]
- MCGREGOR, J. T., R. J. SMITH, & R. E. TALBERT. Interspecific and intraspecific interference of broadleaf signalgrass (*Brachiaria platyphylla*) in rice (*Oryza sativa*). *Weed Sci.* 36: 589–593. 1988a.
- , ——— & ———. Broadleaf signalgrass (*Brachiaria platyphylla*) duration of interference in rice (*Oryza sativa*). *Ibid.* 36: 747–750. 1988b.
- PERNÈS, J., D. COMBES, & R. RÉNÉ-CHAUME. Différenciation des populations naturelles du *Panicum maximum* Jacq. en Côte-d'Ivoire par acquisition de modifications transmissibles, les unes par graines apomictiques, d'autres par multiplication végétative. *Compt. Rend. Acad. Sci. Paris D.* 270: 1992–1995. 1970. [Somatic mutations may be transmitted through vegetative reproduction.]
- , Y. SAVIDAN, & R. RÉNÉ-CHAUME. *Panicum*: structures génétiques du complexe des “Maximae” et organisation de ses populations naturelles en relation avec la spéciation. *Boissiera* 24: 383–402. 1975. [Numerical taxonomic study of selected populations of taxa in the *U. maxima* agamic complex; morphological differentiation not accompanied by differentiation of genomes.]
- RENARD, C., & P. CAPELLE. Seed germination in ruzizi grass (*Brachiaria ruziziensis* Germain & Evrard). *Austral. Jour. Bot.* 24: 437–446. 1976. [= *U. ruziziensis*; see footnote 15.]
- SARKAR, A. K., N. DATTA, U. CHATTERJEE, & R. DATTA. In: IOPB chromosome number reports. XLII. *Taxon* 22: 647–654. 1973. [Counts for two species of *Brachiaria* (including *Urochloa*).]
- SAVIDAN, Y. H. Embryological analysis of facultative apomixis in *Panicum maximum* Jacq. *Crop Sci. Madison* 22: 467–469. 1982. [= *U. maxima*.]

- & J. PERNÈS. Diploid-tetraploid-dihaploid cycles and the evolution of *Panicum maximum* Jacq. *Evolution* **36**: 596–600. 1982. [Variability in *U. maxima* may be perpetuated by continued contact between diploid and tetraploid lines.]
- SCHOLZ, H. Bemerkungen über Gramineen aus dem Berliner Herbar: *Brachiaria* und *Megalachne*. *Willdenowia* **8**: 383–387. 1978.
- SENDULSKY, T. *Brachiaria*: taxonomy of cultivated and native species in Brazil. *Hoehnea* **7**: 99–139. 1978. [Three species introduced in colonial times, seven as pasture grasses more recently, five native species; excellent illustrations and descriptions of each.]
- SHARMA, M. L., & S. KAUR. In: Chromosome number reports. LXIX. *Taxon* **29**: 703–730. 1980. [Counts for seven species of *Brachiaria* (including *Urochloa*).]
- SINGH, D. N. Supernumerary chromosomes in some grasses. *Caryologia* **18**: 547–553. 1965.
- SMITH, L. L. Productivity and nutrient uptake in a tropical *Scirpus/Brachiaria* marsh. *Trop. Ecol. India* **20**: 49–55. 1979.
- SMITH, R. L. Sexual reproduction in *Panicum maximum* Jacq. *Crop Sci. Madison* **12**: 624–627. 1972. [Usually an apomict, but occasional plants reproduce sexually.]
- SOTOMAYOR-RÍOS, A., S. C. SCHANK, & R. WOODBURY. Cytology and taxonomic description of two *Brachiaras* (congoglass and tannergrass). *Jour. Agr. Univ. Puerto Rico* **54**: 390–400. 1970.
- , J. VÉLEZ-FORTUÑO, R. WOODBURY, K. F. SCHERTZ, & A. SIERRA-BRACERO. Description and cytology of a form of signal grass (*Brachiaria brizantha* Stapf) and its agronomic behavior compared to guinea grass (*Panicum maximum* Jacq.). *Ibid.* **44**: 208–220. 1960. [Both now species of *Urochloa*.]
- STÜR, W. W. Reproductive development of the apex of *Brachiaria decumbens* Stapf. *Ann. Bot. II.* **58**: 569–575. 1986. [= *U. decumbens* (Stapf) R. Webster.]
- THOMPSON, R. A., & J. R. ESTES. Anthecial and foliar micromorphology and foliar anatomy of *Brachiaria* (Poaceae: Paniceae). *Am. Jour. Bot.* **73**: 398–408. 1986.
- URBINA, J. A., & L. AVILAN. The kinetic mechanism of phosphoenolpyruvate carboxykinase from *Panicum maximum*. *Phytochemistry* **28**: 1349–1353. 1989. [= *U. maxima*.]
- VAN DER VEKEN, P. Une remarquable espèce nouvelle de *Brachiaria* (Gramineae). *Bull. Jard. Bot. État Brux.* **28**: 77–81. 1958.
- WARMKE, H. E. Cytotaxonomic investigations of some varieties of *Panicum maximum* and of *P. purpurascens* in Puerto Rico. *Agron. Jour.* **43**: 143–149. 1951. [= *U. maxima* and *U. mutica*, respectively.]
- . Apomixis in *Panicum maximum*. *Am. Jour. Bot.* **41**: 5–11. 1954. [= *U. maxima*; facultative apomict; apospory, pseudogamy.]
15. *Eriochloa* Kunth in Humboldt, Bonpland & Kunth, *Nov. Gen. Sp. Pl.* **1**: 78 (folio), 94 (quarto). 1816.

Stoloniferous, decumbent, or caespitose perennials or annuals. Stems with hollow internodes; nodes pubescent (or glabrous). Leaves with sheaths pubescent, at least near base; ligule a fringe of hairs or a fringed membrane; blades linear to lanceolate, flat or folded to involute, glabrous or pubescent, with cuneate or rounded bases, rolled in bud; photosynthesis C₄, biochemical pathway PEP-ck. Inflorescences paniculate, open or contracted, with spike-like primary branches and appressed secondary branches terminating in spikelets. Spikelets lanceolate, dorsiventrally compressed, disarticulating below the glumes, adaxial, secund, short-pedicellate (pedicel apices discoid), solitary or in pairs;

proximal florets staminate or sterile, paleate or epaleate; rachilla pronounced between glumes. Glumes 2, unequal, acute, awned or awnless, 3–9 nerved; proximal glumes minute, at least partly fused with glabrous callus to form a cup-like or bead-like, often black or purple structure; distal glumes equalling or exceeding proximal lemmas, pubescent, acute to short-awned, 5 nerved. Proximal lemmas exceeding and less firm than distal lemmas, pubescent, acute to short-awned, 5 nerved; distal lemmas indurate, rugose, glabrous, mucronate or short-awned, with involute margins and a conspicuous germination flap. Distal paleas awnless, 2 keeled. Lodicules 2. Ovaries with styles free, stigmas red. Caryopses (grains) smooth; endosperm hard, containing only simple starch grains. Base chromosome number 9. LECTOTYPE SPECIES: *Eriochloa distachya* HBK.; see Chase, Proc. Biol. Soc. Wash. **24**: 124. 1911. (Name from Greek, *erion*, wool, and *chloë*, grass, in reference to the hairy spikelets of many species.) — CUPGRASS, CARIBGRASS.

A genus of about 30 species of moist grasslands and open woodlands in tropical and warm-temperate regions of the world. Fifteen species occur in North and Central America, and eight of these have been reported in the Southeast (Shaw & Webster). *Eriochloa* has been divided into two sections by Ohwi. However, the distinction appears to be based largely on pubescence, and the sections are probably not worthy of recognition. No mention of sections is made by Shaw & Webster.

Eriochloa is allied with *Brachiaria* and *Urochloa*, according to most authors. These genera, together with the genera in subtribe Melinidiinae (Hitchc.) Pilger, and *Alloteropsis*, which has leaf anatomy different from other PEP-carboxykinase taxa, are the only taxa in tribe Paniceae to utilize the PEP-carboxykinase decarboxylation system (Hattersley, 1984; Prendergast & Hattersley; Shaw & Smeins, 1981). This similarity in physiology is supported by the morphological similarities revealed in Watson & Dallwitz's analysis. Clayton (1975) suggested that *Eriochloa* is derived from *Brachiaria* (= *Urochloa*, for the most part). The two genera have spikelets oriented adaxially and rugose distal lemmas, in addition to an identical base chromosome number. Clayton (1975) was influenced by the morphology of two exceptional species of *Eriochloa*, *E. biglumis* Clayton, which has a larger proximal glume than usual, and *E. Meyeriana* (Nees) Pilger, which closely resembles *B. mutica* (Forskål) Stapf (= *Urochloa mutica* (Forskål) Nguyen) but has the basal swellings and reduced proximal glumes typical of *Eriochloa*. In fact, he suggested that *E. Meyeriana* and *E. polystachya* were actually the products of introgression between *B. mutica* and various species of *Eriochloa*. No additional evidence in support of this hypothesis has been forthcoming. The much narrower concept of *Brachiaria* accepted by Webster (1987, 1988) does not alter these concepts of relationship, since an expanded *Urochloa* is also a part of this assemblage of similar genera. Butzin's classification (1970) differs in separating *Urochloa* (in subtribe Paspalinae) from *Eriochloa* and *Brachiaria* (both in subtribe Brachiariinae), but this splitting is not justified.

Clayton (1975) also suggested that *Brachiaria callopus* (Pilger) Stapf was similar to certain species of *Eriochloa* because it had globose swellings at the spikelet bases, but he noted that the spikelets were more like those of *Brachiaria* (cf., however, Shaw & Webster). Studies of *Eriochloa* and *B. callopus* suggest that these structures are not homologous (Shaw & Webster). Most authors now place *B. callopus* in *Echinochloa*, which has more distant connections with *Eriochloa* (Shaw & Webster).

Clayton & Renvoize noted that, although *Eriochloa* is distinct, there are still some problems with species limits. Some of these have been resolved in the recent revision of Shaw & Webster. Although no detailed assessment of relationships *within* the genus has yet been attempted, an analysis of epidermal patterns of the callus may provide indications of such relationships. Shaw & Smeins (1979) found three different patterns. Fifteen of the nineteen species they examined have calli in which the apex is heavily striate or plicate. The epidermis at the callus apex is smooth and lacks silica cells, stomata, and macrohairs, while the epidermis at the base of the callus is smooth, regularly pitted with 2- or 4-lobed silica cells, and lacks stomata and macro- and microhairs. Three species (*E. Nelsonii* Scribner & Sm., *E. grandiflora* (Trin.) Bentham, and *E. distachya* Kunth) have calli similar to that described above, except the basal portion lacks silica cells. *Eriochloa polystachya* has a unique pattern among the species examined, in which the upper part of the callus consists of a mass of tissue (lacking stomata and macrohairs, but with scattered bicellular microhairs) that clasps the basal part of the distal glume and proximal lemma, and the basal portion is covered with a rough epidermis. Three- or four-lobed silica bodies are regularly spaced over the entire epidermis.

Eriochloa acuminata (Presl) Kunth var. *acuminata* (*E. gracilis* (Fourn.) Hitchc.), $2n = 36$, (annual, spikelets more than 4 mm long, loosely arranged on branches, leaves and internodes glabrous or nearly so, distal glumes acuminate, distal lemmas acuminate to short-awned) is a weed of ditches, fields, and other disturbed habitats that is spreading through much of the Southeast. It is known from Georgia, Tennessee, Mississippi, and Louisiana in our area. *Eriochloa aristata* Vasey var. *aristata*, $2n = 36$, (annual, panicle branches hairy, spikelets more than 6.4 mm long, distal glumes awned) is a weed of moist disturbed habitats in the Southwest and in Mexico, with one station recorded in the Southeast (Oktibbeha Co., Mississippi; Shaw & Webster). *Eriochloa contracta* Hitchc., prairie cupgrass, $2n = 36$, (annual, leaves and nodes pubescent, primary panicle branches contracted, hairy, with evenly spaced spikelets, distal lemmas awned), a weed of fields and ditches in the Midwest, is an adventive in the western part of our area (Alabama, Mississippi, Louisiana, and Arkansas), as well as in the Southwest. Shaw & Webster consider it to be closely related to *E. acuminata*, but *E. contracta* is distinguished by its long-awned distal lemma and contracted panicle. *Eriochloa fatmensis* (Hochst. & Steudel) Clayton is also similar to *E. contracta*, but it has more

open inflorescences, glabrous nodes, and stouter (0.4-0.6 mm wide vs. 0.4 mm wide or less), glabrous panicle branches, and loosely arranged spikelets. It is an Afro-Asian species that has been introduced into Arizona and Mississippi. Shaw & Webster question whether it is an established component of the North American flora, and I have not been able to verify that it has become established.

Eriochloa Michauxii (Poir.) Hitchc. (incl. *E. longifolia* (Vasey) Vasey), longleaf cupgrass, is represented in the Southeast by var. *Michauxii*, $2n = 36$, and var. *Simpsonii* Hitchc. The species is a perennial and is characterized by spreading primary inflorescence branches and loosely arranged, long, narrow (more than 3.9 mm long, less than 2 mm wide) spikelets, no proximal glumes, and acute or mucronate distal lemmas. Variety *Simpsonii* differs from the typical variety in the sterile (vs. staminate) proximal florets, scabrous or puberulent (vs. pilose) inflorescence branches, and leaves involute and less than 5 mm wide (vs. flat and more than 8 mm wide). Variety *Simpsonii* is a rare endemic of low, wet areas in southwestern Florida (Anderson; Wunderlin *et al.*, 1985), while var. *Michauxii* is more widespread on the Coastal Plain (South Carolina, Georgia, Florida), where it grows in brackish or freshwater marshes, hammocks, and grasslands (Shaw & Webster). There is also an old report from Louisiana, which is quite distant from the remainder of its range in the Southeast (MacRoberts). *Eriochloa polystachya* Kunth, caribgrass, $2n = 36$, (perennial, flowering stems decumbent and rooting at lower nodes, spikelets less than 4 mm long, distal glumes acute, distal lemmas mucronate) occurs in South America, Central America, and the West Indies. It has been introduced into Florida, Mississippi, and Texas as a forage crop, but it is uncertain whether it has become naturalized in North America. *Eriochloa punctata* (L.) Desv. ex Hamilton, $2n = 36$, (perennial, rhizomatous, panicle branches and pedicels glabrous, spikelets more than 4.4 mm long, distal glumes acute to apiculate, distal lemmas awned) grows in coastal marshes and other wet habitats from southwestern Louisiana westward and southward through Central America and to Argentina and Uruguay. It is also known from throughout the West Indies. *Eriochloa villosa* (Thunb.) Kunth, $2n = 54$, (annual, spikelets more than 2 mm wide, distal glumes and lemmas acute) is a weed of fields and disturbed areas in eastern Asia and is an adventive in Florida and Mississippi (Shaw & Webster).

Davidse (1987) suggested that the characteristic swelling at the base of each spikelet in *Eriochloa* serves as an elaiosome, which facilitates diaspore dispersal by ants. He found in *E. acuminata*, *E. distachya*, and *E. Nelsonii* that the swellings contain lipids, indicating a suitable food source for ants. Since this structure is present in all species of *Eriochloa*, the hypothesis of myrmecochory should perhaps be extended to all species in the genus.

Brown (1958a) has found that in *Eriochloa borumensis* Stapf and *E. sericea* (Scheele) Munro ex Vasey, 4-nucleate unreduced embryo sacs develop, and that these lead to apomictic reproduction. Pohl & Davidse

(1971) noted that two populations of *E. polystachya* from Costa Rica had very irregular meiosis and completely sterile pollen, and proposed that these populations probably reproduce through apomixis.

Eriochloa is not particularly important economically. One species, *E. sericea*, is a climax dominant on the Edwards Plateau of Texas where it is considered to be a high quality forage grass (Shaw & Smeins, 1983b). *Eriochloa polystachya* is used in pastures in neotropical areas, but it has not been successfully introduced into North America for this purpose (Shaw & Webster). *Eriochloa distachya*, cupgrass, has been used for treating eye diseases in Venezuela (Morton). *Eriochloa acuminata*, *E. contracta*, *E. pacifica* Mez, *E. procera* (Retz.) C. E. Hubb., and *E. punctata* are weeds in tropical areas of the world (Holm *et al.*; Shaw & Webster). *Eriochloa punctata* is also a host for strain A of the maize dwarf mosaic virus (Rosenkranz).

REFERENCES:

Under references for tribe see ANDERSON; BLAKE; BOLKHOVSKIKH *et al.*; BROWN (1958a); BUTZIN (1970); CHASE (1911); CHIPPINDALL; CLAYTON (1980); CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1975, 1979); HATTERSLEY (1984); HOLM *et al.*; JONES & COILE; MACROBERTS; MORTON; OHWI; POHL (1980); POHL & DAVIDSE (1971); PRENDERGAST & HATTERSLEY; ROSENKRANZ; E. SMITH; TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); WUNDERLIN; and WUNDERLIN *et al.* (1985).

- ARRIAGA, M. O. Interpretación del ornamento del antecio de *Eriochloa* (Poaceae). Bol. Soc. Argent. Bot. **25**: 131-141. 1987. [Three types of ornamentation of the distal floret bracts described: warts, papillae, and compound papillae; warts are composed of SiO₂.]
- CLAYTON, W. D. New species of *Eriochloa* from Africa. Kew Bull. **30**: 107-109. 1975. [Discussion of aberrant taxa, their possible origins and relationships.]
- EVERS, R. A. Illinois flora: notes on *Eriochloa* and *Jussiaea*. Rhodora **61**: 307-309. 1959. [*E. gracilis* newly adventive in the state.]
- GOULD, F. W. *Eriochloa* in Arizona. Leafl. West. Bot. **6**: 50, 51. 1950. [Four taxa keyed; *E. Lemmonii* Vasey & Scribner var. *gracilis* (Fourn.) Gould, comb. nov.]
- GRIF, V. G. New chromosome numbers in flowering plants. (In Russian.) Bot. Zhurn. **50**: 1133-1135. 1965. [*E. succincta* (Trin.) Kunth from Caucasus, 2n = 36.]
- HSU, C.-C. Preliminary chromosome studies on the vascular plants of Taiwan (IV). Counts and systematic notes on some monocotyledons. Taiwania **16**: 123-136. 1971. [*E. procera*, n = 9.]
- SHAW, R. B., & F. E. SMEINS. Epidermal characteristics of the callus in *Eriochloa* (Poaceae). Am. Jour. Bot. **66**: 907-913. 1979. [Three types.]
- & ———. Some anatomical and morphological characteristics of the North American species of *Eriochloa* (Poaceae: Paniceae). Bot. Gaz. **142**: 534-544. 1981. [Leaf blade anatomy; scanning electron microscopy of leaf blade epidermis; lemma and palea surface features.]
- & ———. Additional observations of the callus in *Eriochloa*. Isleya **2**: 15-19. 1983a. [Callus of *Eriochloa* is a unique structure that may incorporate remnants of the proximal glume.]
- & ———. Herbage dynamics and forage quality of Texas cupgrass (*Eriochloa sericea*). Jour. Range Manage. **36**: 666-672. 1983b.

- & R. D. WEBSTER. The genus *Eriochloa* (Poaceae: Paniceae) in North and Central America. *Sida* **12**: 165–207. 1987. [Excellent monograph of the North American taxa, with illustrations of most taxa.]
- TERRELL, E. E. Adventive records of *Eriochloa contracta* (Gramineae) in the United States. *Sida* **5**: 48. 1972. [New state records for Alabama, Indiana, Mississippi.]

16. **Paspalum** Linnaeus, *Syst. Nat.* ed. 10: 855. 1759.

Rhizomatous, stoloniferous, decumbent, or caespitose perennials or annuals. Stems from bulbous or non-bulbous bases; internodes solid or hollow; nodes glabrous or pubescent. Leaves with sheaths glabrous or pubescent; ligule a fringed or unfringed membrane or a fringe of hairs; blades linear to linear-lanceolate, flat, folded, or involute, glabrous to pubescent, with cuneate to truncate bases, rolled in bud; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences paniculate, primary branches 1–60, digitate, subdigitate, or pinnately racemose, terminating in spikelets or not [with subterranean cleistogamous spikelets in *P. amphicarpum*]; rachides narrow, flattened, or winged. Spikelets orbicular to lanceolate, dorsiventrally compressed, planoconvex, disarticulating below the glumes, abaxial, secund, subsessile or pedicellate (pedicel apices oblique, truncate, discoid, or cupuliform), solitary or paired (when paired, the lower often abortive), biseriate; proximal florets staminate or sterile, epaleate. Calli undifferentiated. Glumes 1 or 2 [0], unequal, glabrous to pubescent or glandular-pubescent, awnless; proximal glumes, if present, 0–1 nerved; distal glumes membranaceous, obtuse to acuminate, [0] 2–7 nerved (midnerve often absent). Proximal lemmas equalling and similar in texture or less firm than distal lemmas, glabrous to pubescent [margins fimbriate in *P. fimbriatum*], obtuse to acuminate, awnless, 3–5 nerved; distal lemmas indurate, smooth or striate, glabrous, green to brown, obtuse, awnless, 3–5 nerved, with involute margins and a conspicuous germination flap. Distal paleas indurate, obtuse, awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red. Caryopses (grains) small, not grooved, smooth; endosperm hard, containing only simple starch grains. Base chromosome number 10. LECTOTYPE SPECIES: *Paspalum dimidiatum* L. = *Paspalum dissectum* (L.) L.; see Chase, *Proc. Biol. Soc. Wash.* **24**: 137. 1911. (From Greek, *paspalos*, the name of a millet used by the ancient Greeks.) — PASPALUM, DALLIS GRASS, KNOTGRASS, LONGTOM, BAHIA GRASS, VASEY GRASS.

A genus of about 250 species, mostly of the Neotropics but with a few species in the Old World tropics, occurring in a wide array of habitats, including dry and wet woodlands, grasslands, and wetlands, disturbed areas, and cultivated fields. The center of diversity of the genus is in the American tropics; Brazil is particularly rich in species (Chase, 1929; Pohl, 1980).

Paspalum is a readily recognizable genus. It is characterized by an inflorescence consisting of racemose branches and by plano-convex,

abaxial spikelets in which the proximal glumes are generally lacking and the distal lemmas are obtuse, indurate, and have involute margins. The spikelets are biseriate and secund. The genus has a close phenetic (and perhaps also phylogenetic) resemblance to *Axonopus*. Chase (1906) and Webster (1988) noted that the only truly reliable difference between these genera is in spikelet orientation, with *Axonopus* having adaxial spikelet orientation. This difference in ontogenetic terms involves rotation of a pedicel 180 degrees. The genetic basis of this is crucial to the interpretation of generic limits and relationships in tribe Paniceae.

The phenetic analysis of Watson & Dallwitz indicates that *Echinochloa*, *Brachiaria* (= *Urochloa*), *Axonopus*, and *Panicum* are most similar to *Paspalum*. All but *Urochloa* share a common C₄ acid decarboxylation system (NADP-malic enzyme; Brown, 1977). Clayton & Renvoize place *Paspalum* in subtribe Setariinae. Tsvelev (1976) splits the subtribes more finely and places *Paspalum* in subtribe Brachiariinae. Pohl (1980) agreed with the phenetic relationships documented by Watson & Dallwitz and added *Paspalidium* to the list of close relatives. *Reimarochloa* was separated from *Paspalum* by Hitchcock (1909). Fournier considered certain tropical American species to be intermediate between *Paspalum* and *Panicum*, and placed them in the segregate genus *Dimorphostachys* Fourn. (e.g., *P. monostachyum*). These species are now included in *Paspalum*, but this serves to point out the close phenetic relations between some groups of species within these two genera.

Paspalum has been divided into various infrageneric groups, ranging from formal subgenera, sections, and subsections to informal species groups. Nees and Pilger (1929, 1940) divided the genus into sections. Their sections do not always coincide, and Pilger (1929), without apparent reason, substituted new names for some of the sections already validly published by Nees. Most such cases involve groups that contain no North American species. For example, he renamed sect. *Lanigeri* Nees, sect. *Erianthum* Pilger, and cited the former as a synonym. Pilger recognized a total of eight sections. Clayton & Renvoize claim that Pilger (1940) recognized sect. *Diplostachys* (containing three-quarters of all species of *Paspalum*), but this, in fact, is not one of the sections mentioned by Pilger (1929, 1940). Bentham and Hackel followed Nees' sectional classification and divided sect. *Eupaspalum* (= sect. *Paspalum*) into several subsections. Most of these had been recognized at various ranks by previous authors.

The North American species fall into two of Pilger's sections (sect. *Eupaspalum* (= sect. *Paspalum*) and sect. *Cymatochloa* (Schlecht.) C. Müller). Chase (1929) considered the taxa in both of these sections to be in informal species groups within subg. *Paspalum*. She recognized two subgenera for *Paspalum* as it is represented in North America, subg. *Paspalum* and subg. *Ceresia* (Pers.) Reichenb.), but the latter contains no species in the United States or Canada.

Considering the size of the genus and its economic importance in the subtropics and tropics, surprisingly little taxonomic work has been devoted to it. There is no recent worldwide monograph, and there is no modern infrageneric classification scheme. The infrageneric categories that have been recognized are based on rachis morphology, spikelet pubescence, distal glume morphology, and distal lemma texture (Clayton & Renvoize). The only usable scheme for North American species is that of Chase (1929). She recognized many informal species groups that have no nomenclatural standing. Since many species are variable, and since most combinations of character states can exist, this informal scheme may, in fact, be the most reasonable approach to take from a practical viewpoint. Much effort is needed to determine infrageneric relationships and to reflect them in a classification scheme. Recent attempts to assess genomic relationships of economically important taxa are a first step in this direction (see Bennett & Bashaw; Burson, 1978, 1979, 1981a, b, 1985; Burson & Bennett, 1972; Burson *et al.*; Forbes & Burton; Hanna & Burton; Norrmann *et al.*; Quarín & Burson).

The earliest monograph of North American *Paspalum* is that of Le Comte. It treats 18 species, a few of which were newly described. Vasey commented on all of Le Comte's species and their variability. The most important monograph of North American *Paspalum* (Chase, 1929) treated 35 species (in 12 informal species groups) for the southeastern United States. Chase (1929) did much to improve species delimitations, but she employed a rather narrow species concept. Some of those species have been reduced in rank or submerged in the synonymy of more inclusive species concepts. A case in point is the *P. setaceum* Michx. complex, in which she recognized nine species (*P. longepedunculatum* Le Comte, *P. debile* Michx., *P. supinum* Bosc, *P. psammophilum* Nash, *P. stramineum* Nash, *P. pubescens* Muhl., *P. ciliatifolium* Michx., *P. propinquum* Nash, and *P. rigidifolium* Nash), at the same time acknowledging that the characters used to delineate these, such as pubescence patterns and spikelet shape and dimensions, were quite variable. Shinnars (1954) also noted their variability and indistinctness. More recently, Banks (1966b) treated all of them under *P. setaceum*, although he maintained several at the varietal rank.

Group Dissecta contains *Paspalum dissectum*, the type species of the genus. Species in this group are annuals or perennials, and the plants usually consist of branched and straggling culms. Other characteristics include broadly winged, green inflorescence branch rachides, glabrous (or in *P. repens* Berg. minutely puberulent) spikelets, and pale floret bracts when in fruit. Three species of this group occur in the Southeast: *P. dissectum*, mudbank paspalum, $n = 20$ (New Jersey to Illinois, south through our area to the Gulf Coast, Cuba; rare north of South Carolina); *P. acuminatum* Raddi, brook paspalum (central Florida, southern Mississippi, Louisiana, and Texas, south through Central and South America to Argentina); and *P. repens* (*P. fluitans*

(Ell.) Kunth), water paspalum (Virginia to Indiana and Kansas, south through our region and Central and South America to Argentina).

Group *Disticha* includes perennial creepers with racemose inflorescence branches in pairs and pointed spikelets. *Paspalum vaginatum* Sw.,¹⁶ seashore paspalum, $n = 10$, is nearly circumtropical, and in our area it occurs near the coast of North Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana. *Paspalum distichum* L. (*P. paspalodes* (Michx.) Scribner), knotgrass, $n = 20, 30, 2n = 48$, is more widespread, occurring throughout the Southeast and as far north as New Jersey and Pennsylvania in the East, and westward to California, Oregon, and Washington in the West.

Group *Livida* consists of perennials with compressed culms, flat leaf blades, and spikelets 2–3 mm long. Chase (1929) suggested that this group was artificial. In our area the following two species belong to this group: *Paspalum pubiflorum* Rupr. ex Fourn., hairyseed paspalum, $n = 30, 2n = 60, 64$ (southwestern North Carolina, Ohio, and Indiana, to northern Florida, Kansas, and Texas, south to Mexico and Cuba) and *P. lividum* Trin., longtom, $n = 20$ (Alabama, Louisiana, and Texas, south through Central America and northern South America to Argentina and Peru).

Group *Notata* is represented in our area by *Paspalum notatum* Flügge, Bahia grass, $n = 10, 20$, and *P. minus* Fourn., mat paspalum, $n = 20$ (Chase, 1929; Banks, 1966a). They are perennials with leafy bases, compressed culms, and solitary spikelets along the rachides. *Paspalum notatum* is a species of Central and South America that has been widely introduced in our area from North Carolina to Arkansas, south to Florida and Texas. It has also been collected as an adventive in New Jersey. Varietas *notatum* and var. *Saurae* Parodi have been introduced into the Southeast (Clewett; Radford *et al.*; Wunderlin). *Paspalum minus*, a West Indian species, has recently become naturalized and is known from Alabama, Mississippi, and Louisiana in our area.

Group *Setacea* contains the hardiest of the North American species, including the *Paspalum setaceum* complex, thin paspalum, $n = 10$, which extends north to southwestern Ontario (Crins *et al.*). Plants of the *P. setaceum* complex are highly variable, and a number of varieties are recognized (Banks, 1966b). The following are known from our area: vars. *ciliatifolium* (Michx.) Vasey, *longepedunculatum* (Le Comte) Wood, *Muhlenbergii* (Nash) D. Banks, *rigidifolium* (Nash) D. Banks, *setaceum*, *stramineum* (Nash) D. Banks, *supinum* (Bosc) Trin., and *villosissimum* (Nash) D. Banks. Plants of *P. setaceum* are perennials, with very short rhizomes or knotted bases, compressed culms, flat leaf blades, long-ciliate ligules, and terminal and axillary inflorescences consisting of slender racemose branches. The spikelets

¹⁶Wunderlin lists *P. distichum* and *P. paspalodes* from central Florida. However, Guédès resolved the nomenclatural problem that resulted in the misapplication of these names. The correct names for these species should be *P. vaginatum* Sw. and *P. distichum* L., respectively (see Wunderlin *et al.*, 1988).

are paired and crowded on the rachides, and the distal floret bracts are smooth and lustrous.

Two members of the Decumbentes group occur in the Southeast: *Paspalum monostachyum* (Kunth) Vasey, gulfdune paspalum (Florida, Louisiana) and *P. Langei* (Fourn.) Nash, rustyseed paspalum, $n = 20, 30$ (Florida to Texas along the Gulf Coast). These are branched perennials, with terminal and axillary inflorescences consisting of one to many racemose branches, rachides narrow (ca. 1 mm wide), spikelets paired, and a proximal glume often present on at least one spikelet of each pair.

Group Caespitosa is comprised of tufted perennials with few to many racemose inflorescence branches and elliptic spikelets. *Paspalum Blodgettii* Chapman, coral paspalum; *P. caespitosum* Flügge, blue paspalum, $n = 10$; *P. laxum* Lam.; and *P. Nicorae* Parodi occur from Florida southward into the West Indies, Central America, and/or South America. *Paspalum Nicorae* has recently escaped along roadsides and in pastures in central Florida (Wunderlin *et al.*, 1985).

Paspalum conjugatum Berg., sour paspalum, $n = 20, 40$, a circumtropical species, is the only representative of the Conjugata group in the Southeast (Florida, Alabama, Louisiana, and Texas). It is a stoloniferous perennial with lax, flat leaf blades and two slender yellow racemes.

Group Dilatata contains two species in the Southeast: *Paspalum dilatatum* Poir., Dallis grass, $n = 20, 25, 30$, and *P. Urvillei* Steudel, Vasey grass, $n = 20, 30$, both introduced from South America, and both widespread in the region. Members of this group are robust perennials, with flat leaves, few to numerous racemose inflorescence branches, and paired, flat spikelets that are conspicuously ciliate.

Group Laevia contains *P. laeve* Michx. (including *P. longipilum* Nash, *P. circulare* Nash), field paspalum, $n = 20$, another widespread North American species, the range of which extends into temperate regions. In addition *P. praecox* Walter (including *P. lentiferum* Lam.), early paspalum, $n = 10, 20$, grows on the Atlantic and Gulf Coastal Plains from Virginia to Florida and Texas. It has also been reported from Arkansas (E. Smith). Species in this group are perennials with short rhizomes and tall, compressed stems, inflorescences of few to several racemose branches, and spikelets usually solitary along the rachides, broadly oval to circular, and glabrous.

Group Floridana consists of robust perennials with simple culms, flat leaf blades, and large inflorescences with large, turgid, glabrous spikelets. *Paspalum floridanum* Michx. (including *P. difforme* Le Comte, *P. giganteum* Baldwin ex Vasey), Florida paspalum, $n = 60, 80$, is our only representative of this group. It occurs from New Jersey westward to Missouri and Kansas, and southward to Florida and eastern Texas.

The Plicatula group contains annuals and perennials that often have anthocyanic stems and leaf sheaths. The large inflorescences bear spikelets that turn brown to dark greenish-brown at maturity. Bracts of the distal florets are dark brown and lustrous. *Paspalum plicatulum* Michx., brownseed paspalum, $n = 10, 20$, (perennial, spikelets paired)

occurs from South Carolina to Florida and Texas along the Atlantic and Gulf Coastal Plain, and southward through Central and South America to Argentina. The closely related *P. convexum* Flügge (annual, spikelets solitary) has been reported from several sites in Louisiana (MacRoberts). *Paspalum Boscianum* Flügge, bull paspalum, $n = 20$, occurs from Virginia and eastern Arkansas, south to Brazil, and there is also a record from Pennsylvania.

Paspalum intermedium Morong, of the South American group Quadrifaria (Norrman *et al.*), is known from the Southeast in Georgia (Jones & Coile). It contains a diploid, sexual, self-incompatible race and a tetraploid, facultatively apomictic race. Another South American species, *P. hydrophilum* Henr., has been collected in irrigation ditches in southwestern Louisiana (MacRoberts).

Paspalum bifidum (Bertol.) Nash, pitchfork paspalum, a species of uncertain placement, occurs from Virginia to central Florida and Texas. Chase (1929) suggested that its affinities are with *Panicum*.

Paspalum contains some of the most important tropical forage grasses, and for this reason, great efforts have been made to develop cultivars and hybrids with increased yields that can withstand grazing, tolerate diseases, and grow in more stressful environments (Bennett & Bashaw; Burton, 1940). An ancillary benefit of this work has been a greatly improved understanding of the reproductive systems, genetic barriers, and genomic relationships of some of the species. Self-pollination occurs in some sexually reproducing species and may account for the uniformity of morphology in the progeny (Banks, 1964b; Connor, 1981). Self-pollination may significantly reduce seed set, but such seeds yield plants that are just as vigorous as those resulting from cross-pollination, at least in some populations of *P. notatum* (Burton, 1948b). However, the evidence for self-compatibility is contradictory in *P. notatum*, with Hodgson (1949a) considering plants of that species to be self-incompatible. The South American *P. yaguaronense* Henr. (= *P. glaucescens* Hackel; Renvoize) is also generally self-incompatible (Pritchard, 1962), as is the diploid *P. hexastachyum* Parodi (Quarin & Hanna, 1980). Unfortunately, no detailed genetic analyses of the self-incompatibility system in *Paspalum* have been made.

Polyploidy and apomictic reproduction are common features in the genus. Hunziker & Stebbins estimate that about 64 percent of the species contain polyploid populations. *Paspalum dilatatum* is the most thoroughly studied species with regard to breeding systems. Six biotypes have been characterized within this species (Bashaw & Forbes; Fernandes *et al.*; B. Smith). One of these is tetraploid ($2n = 40$) and has regular meiosis, with 20 bivalents routinely forming, and is considered to be the probable ancestral type from which the other biotypes arose. The plants grow erect, and have yellow anthers and pubescent spikelets. Another tetraploid (meiosis irregular) with very low bivalent formation and laggards common at anaphase-I, is semiprostrate and has purple anthers. There are also yellow- and purple-anthered pentaploids ($2n = 50$) that form 20 bivalents and 10 univalents during

meiosis, as well as hexaploids ($2n = 60$) that have variable numbers of univalents and trivalents (race "uruguayiana") or uniformly produce 60 univalents (race "torres"). The purple-anthered tetraploid and all pentaploids and hexaploids appear to be obligate apomicts, reproducing by apospory with pseudogamy, while the yellow-anthered tetraploid reproduces sexually. Fernandes and coworkers have suggested that the "torres" race might have developed through the union of two unreduced gametes, one from a tetraploid (presumably sexual *P. dilatatum*), and the other from an octoploid such as the sympatric *P. virgatum*.

Hybridization experiments with tetraploid *Paspalum dilatatum* and other species have shown that the sexually reproducing race is an allotetraploid and that it shares one genome with *P. intermedium* and the other with *P. Jurgensii* Hackel (both are diploid, $2n = 20$; Burson, 1978). Burson (1979) showed that *P. Urvillei* (of the same species group) has the same genomic constitution as *P. dilatatum*. He suggested that the tetraploids may have originated from the same progenitors (*P. intermedium* and *P. Jurgensii*). The phenotypic differences between *P. dilatatum* and *P. Urvillei* may have resulted from genetic changes accumulating through time. In Brazil, where both are native, introgression takes place (Burson, 1979), suggesting to me that they are not distinct species. Crosses between *P. Urvillei* and *P. vaginatum* indicate very little homology of genomes (Burson & Bennett, 1972). This result is also in accord with Chase's assignment (1929) of the two species to different groups. Similar confirmation of genetic distance between species groups has been obtained in crosses between *P. Jurgensii* and *P. setaceum* var. *ciliatifolium*, *P. Jurgensii* and *P. vaginatum* (Burson, 1981a), *P. intermedium* and *P. notatum*, and *P. notatum* and *P. vaginatum* (Burson, 1981b). On the other hand, closeness of relationship within species groups is supported by relatively high bivalent formation in hybrids between *P. notatum* var. *Saurae* and *P. pumilum* (Quarín & Burson, 1983).¹⁷

Attempts have been made to determine the origins of the additional genomes in higher ploidy level races of *Paspalum dilatatum*. The sexual tetraploid, *P. dilatatum*, was crossed with the aposporous hexaploid, *P. durifolium* Mez (Quadrifaria group), to generate pentaploids. Although one genome (that derived from *P. Jurgensii*) is homologous, and the other genome is partially homologous, Burson (1985) concluded that these hybrids were different enough in morphology from *P. dilatatum* pentaploids to rule out *P. durifolium* as a progenitor of the common pentaploid biotype of *P. dilatatum*.

Several other crops or their relatives exhibit high seed set in spite of total chromosomal asynapsis at meiosis and pollen sterility. *Paspalum Commersonii* Lam., a close relative of the cultivated Old World species *P. scrobiculatum* L. (Clayton, 1975), is hexaploid ($2n = 60$), but produces much seed through apomixis (Christopher *et al.*).

¹⁷A contradictory result had been obtained in an earlier cross between these two species (Burson, 1981b).

Aneuploidy is infrequent in *Paspalum*. In plants of *P. dilatatum* from India, $n = 27$ has been reported (Mehra & Chaudhary, 1976), and in root tips of plants of this species from Nigeria and France chromosome numbers ranged from $2n = 40$ to 63 (Singh & Godward). In *P. pubiflorum* from Mexico, $2n = 64$ has been recorded, in addition to the euploid number of $2n = 60$ (Gould, 1966). In *P. distichum* from Florida, $2n = 48$ has been reported (Burton, 1942). The divergent base number in *P. hexastachyum* ($n = x = 6$) probably arose through some sort of aneuploid event. This species is now cytologically stable and reproduces sexually (Quarín & Hanna, 1980).

One additional reproductive system has evolved in a species of *Paspalum*. In *P. amphicarpum* Ekman subterranean spikelets containing cleistogamous flowers are produced, in addition to the chasmogamous flowers in spikelets of the aerial inflorescences (Campbell *et al.*; Clayton & Renvoize). This is a rare development in grasses, but it has arisen independently in one other panicoid genus, *Amphicarpum*.

Flowering induction in *Paspalum dilatatum* and its relatives has also been examined. Long days (14 hours or more of sunlight) are generally required to induce regular flowering behavior. Flowering is also enhanced by temperatures above 21°C (70°F) in *P. dilatatum*, *P. Urvillei*, and *P. malacophyllum* Trin. *Paspalum Urvillei* is most tolerant of cool temperatures and flowers, at least occasionally, at temperatures as low as 5.5°C (42°F) (Bennett, 1959; Knight). Pollination is necessary for full caryopsis development in almost all species of *Paspalum*, regardless of reproductive method. Sexually reproducing species obviously require pollination for fertilization, but most apomictic species in the genus also require pollination for the development of the endosperm (pseudogamy). Chao (1971, 1977a, b, 1979, 1980) has thoroughly characterized pseudogamy in *P. conjugatum*.

Although there is good reason to believe that most species of *Paspalum* are largely anemophilous, Adams and coworkers have made a case for partial entomophily in *P. dilatatum*. Halictid bees were observed visiting plants in an Oklahoman population and gathering pollen regularly. The number of pollen grains per stigma was significantly greater on spikelets of racemes exposed to both wind and insects than on spikelets of racemes protected from insect visits. Spikelets of racemes exposed to both pollination agents set significantly more seed than spikelets exposed only to the wind. Karr noted a close association between noctuid moths and the inflorescences of *P. virgatum*. He suspected that moths might be attracted to a fluid secreted by the open spikelets and wondered whether an adaptation to moth pollination had developed in this population. However, it was later determined that the source of the exudate was likely from *Claviceps paspali* Stev. & Hall, a fungus that causes ergot, and that the moths were probably feeding on the secretions of the fungus. Any pollination that might be accomplished would be fortuitous (Pohl *et al.*, 1979), especially since *Paspalum* species shed pollen during the day, as far as is known (cf. Adams *et al.*).

Some species of *Paspalum* (e.g., *P. scrobiculatum*) produce substances that induce symptoms in lab animals resembling those of human Parkinson's disease, including tremors and facial and limb rigidity. The active compound behaves like an alkaloid chemically and clinically but has not been characterized analytically (Bhide & Aimen). The actual source of this alkaloid-like toxin has recently been questioned, since plants producing this compound are also infected by a smut fungus (Bor, 1960; De Wet *et al.*, 1983). In any case the presence of this compound is of importance because *P. scrobiculatum* is cultivated as a grain crop in several areas in the tropics.

Some *Paspalum* species produce sulfated flavonoids, which are of rather restricted distribution among the angiosperms. In grasses, only 17 percent of the species surveyed (274) possessed this substitution pattern (Harborne & Williams).

The dispersal ecology of most *Paspalum* species is very poorly known. Some speculations have appeared in the literature. For example, the recent occurrences of *P. minus* from Texas to Alabama along the Gulf of Mexico have been attributed to possible long-distance dispersal of seeds from West Indian sources via hurricanes (Banks, 1966a), although the suggestion was also made that seed may have been introduced as an impurity in samples of *P. notatum* seed (a more likely option!).

Some of the aquatic species, such as *Paspalum repens*, may form massive floating mats. Chunks of these mats may be torn away and are then dispersed by river currents (Arber, 1934). A few species have prominent spikelet hairs, or even winglike spikelet margins (e.g., *P. fimbriatum* Kunth) that may assist in the dispersal of fruits by wind (Davidse, 1987).

A fossil distal floret of a *Paspalum* has been reported from a deposit of Pleistocene age in Louisiana (Thomasson, 1987).

The economic importance of several species of *Paspalum* has already been noted briefly. Much effort has gone into developing resistant, hardy, and uniform varieties of *P. dilatatum*. It is a valuable pasture grass throughout the tropics for dairy cattle. Several North American species have been characterized as good forage species (e.g., *P. laeve*, *P. setaceum*). *Paspalum notatum* is used around the world in warmer regions as a pasture grass. Several species are also good sandbinders (e.g., *P. distichum*, *P. vaginatum*). *Paspalum conjugatum* forms good turfs for golf courses, but it is not a favorite of grazing ungulates (Chase, 1929). *Paspalum scrobiculatum*, kodo millet, was domesticated in India about 3000 years ago and is still harvested as a cereal grain there and in West Africa (De Wet *et al.*, 1983). It is highly variable, but no races seem to have been differentiated, and Clayton (1975) merged several segregates (including *P. Commersonii* and *P. orbiculare* Forster f.) into one polymorphic species. Continual hybridization of cultivated selections and wild types that invade cultivated fields probably contributes to this lack of differentiation.

Some species have been used in folk medicines in the Neotropics. *Paspalum conjugatum* has been used in baths for treating malaria and

also as a remedy for fevers, influenza, pleurisy, pneumonia, fatigue, and tuberculosis (in concoctions with *Opuntia* and wood ash). *Paspalum vaginatum* has been used as a diuretic, and to treat patients with liver and urinary tract ailments, fever, and high blood pressure (Morton).

Paspalum dilatatum is a weed in many areas, for example olive (*Olea europaea* L.) groves, grasslands, and ruderal areas in Yugoslavia (Ilijanic & Topic). Many other species are listed as weeds (some of them serious ones) in various parts of the tropics (Holm *et al.*). *Paspalum alnum* Chase, *P. malacophyllum*, and *P. scrobiculatum* may serve as hosts for various viral diseases of crops; *P. alnum* for the A-strain of maize dwarf mosaic virus, *P. malacophyllum* for this and the sugarcane mosaic virus, and *P. scrobiculatum* for sugarcane mosaic and both A- and B-strains of maize dwarf mosaic virus (Rosenkranz).

REFERENCES:

- Under references for tribe see ARBER (1934); BENTHAM; BOLKHOVSKIKH *et al.*; BOR (1960); BROWN (1977); CAMPBELL *et al.*; CHASE (1906, 1911); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; CONNOR (1981); DAVIDSE (1987); GOULD (1966, 1975, 1979); HACKEL; HARBORNE & WILLIAMS; HITCHCOCK (1909); HITCHCOCK & CHASE (1910, 1951); HOLM *et al.*; HUNZIKER & STEBBINS; JONES & COILE; MACROBERTS; MEHRA & CHAUDHARY (1976); MORTON; NASH (1913); PILGER (1940); POHL (1980); RADFORD *et al.*; RENVOIZE; ROSENKRANZ; SHINNERS (1954); SILVEUS; SINGH & GODWARD; E. SMITH; THOMASSON (1987); TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); WUNDERLIN; and WUNDERLIN *et al.* (1985).
- ADAMS, D. E., W. E. PERKINS, & J. R. ESTES. Pollination systems in *Paspalum dilatatum* Poir. (Poaceae): an example of insect pollination in a temperate grass. *Am. Jour. Bot.* **68**: 389-394. 1981.
- ANDERSON, D. E. In: Documented chromosome numbers of plants. *Madroño* **17**: 266-268. 1964. [*P. distichum* from California, $n = 20$.]
- BANKS, D. J. Cytological studies in *Paspalum*, group *Setacea* (Gramineae). *Sida* **1**: 306-312. 1964a. [All counts $n = 10$.]
- . Chromosome counts for *Paspalum*. *Rhodora* **66**: 368-370. 1964b. [Five spp.]
- . Taxonomy of *Paspalum setaceum* (Gramineae). *Sida* **2**: 269-284. 1966a. [Several species treated as varieties within *P. setaceum*; range maps and photographs of spikelets of each variety included; *P. setaceum* is the correct epithet of several that Michaux published simultaneously, since it is the first name under which the other species were submerged.]
- . *Paspalum minus* (Gramineae) in Louisiana and Mississippi. *Rhodora* **68**: 94-96. 1966b.
- BASHAW, E. C., & I. FORBES. Chromosome numbers and microsporogenesis in Dallisgrass, *Paspalum dilatatum* Poir. *Agron. Jour.* **50**: 441-445. 1958. [Four biotypes; one with regular meiosis, the others with irregular meiosis and presumed to be apomictic.]
- & E. C. HOLT. Megasporogenesis, embryo sac development and embryogenesis in Dallisgrass, *Paspalum dilatatum* Poir. *Ibid.* 753-756. 1958. [One biotype reproduces sexually; another is an obligate aposporous apomict requiring pseudogamy.]
- BENNETT, H. W. Embryology of *Paspalum dilatatum*. *Bot. Gaz.* **106**: 40-45. 1944.
- . The effect of temperature upon flowering in *Paspalum*. *Agron. Jour.* **51**: 191-193. 1959.

- & E. C. BASHAW. An interspecific hybrid in *Paspalum*. Jour. Hered. **51**: 81–85. 1960. [*P. dilatatum* × *P. malacophyllum*.]
- BHIDE, N. K., & R. A. AIMEN. Pharmacology of a tranquilizing principle in *Paspalum scrobiculatum* grain. Nature **183**: 1735, 1736. 1959. [Toxic alkaloid-like substance induces Parkinson-like symptoms in lab animals.]
- BURSON, B. L. Genome relations between *Paspalum conspersum* and two diploid *Paspalum* species. Canad. Jour. Genet. Cytol. **20**: 365–372. 1978.
- . Cytogenetics of *Paspalum Urvillei* × *P. intermedium* and *P. dilatatum* × *P. paniculatum* hybrids. Crop Sci. Madison **19**: 534–538. 1979. [Genome relations support taxonomic classification.]
- . Cytogenetic relationships between *Paspalum Jurgensii* and *P. intermedium*, *P. vaginatum*, and *P. setaceum* var. *ciliatifolium*. Ibid. **21**: 515–519. 1981a.
- . Genome relations among four diploid *Paspalum* species. Bot. Gaz. **142**: 592–596. 1981b. [*P. intermedium*, *P. notatum*, *P. pumilum*, *P. vaginatum*.]
- . Cytology of *Paspalum chacoense* and *P. durifolium* and their relationship to *P. dilatatum*. Ibid. **146**: 124–129. 1985.
- & H. W. BENNETT. Cytology and reproduction of three *Paspalum* species. Jour. Hered. **61**: 129–132. 1970. [*P. guaraniticum*, *P. intermedium*, *P. quadrifarium*.]
- & ———. Chromosome numbers, microsporogenesis, and mode of reproduction of seven *Paspalum* species. Crop Sci. Madison **11**: 292–294. 1971.
- & ———. Cytogenetics of *Paspalum Urvillei* × *P. Juergensii* and *P. Urvillei* × *P. vaginatum* hybrids. Ibid. **12**: 105–108. 1972.
- , H.-S. LEE, & H. W. BENNETT. Genome relations between tetraploid *Paspalum dilatatum* and four diploid *Paspalum* species. Ibid. **13**: 739–743. 1973.
- BURTON, G. W. A cytological study of some species in the genus *Paspalum*. Jour. Agr. Res. **60**: 193–197. 1940.
- . Artificial fog facilitates *Paspalum* emasculation. Jour. Am. Soc. Agron. **40**: 281, 282. 1948a.
- . The method of reproduction in common Bahia grass, *Paspalum notatum*. Ibid. **40**: 443–452. 1948b. [Apomixis.]
- . Effect of environment on apomixis in bahia grass. Crop Sci. Madison **22**: 109–111. 1982. [Day length, moisture stress, low soil fertility had no effect.]
- CHAO, C.-Y. A periodic acid-Schiff's substance related to the directional growth of pollen tube into embryo sac in *Paspalum* ovules. Am. Jour. Bot. **58**: 649–654. 1971.
- . Megasporogenesis and megagametogenesis in *Paspalum Commersonii* and *P. longifolium* at two polyploid levels. Bot. Not. **127**: 267–275. 1974. [*P. Commersonii* aposporic at hexaploid and dodecaploid levels; *P. longifolium* apparently not aposporic, but produces unreduced megaspores; both species always produce 8-nucleate embryo sacs.]
- . Light microscopic detection of PAS-positive substances with thiosemicarbazide in freeze-substituted ovaries of *Paspalum longifolium* before pollination. Histochemistry **54**: 159–168. 1977a.
- . Further cytological studies of a periodic acid-Schiff's substance in the ovules of *Paspalum orbiculare* and *P. longifolium*. Am. Jour. Bot. **64**: 921–930. 1977b.
- . Histochemical study of a PAS substance in the ovules of *Paspalum orbiculare* and *P. longifolium*. Phytomorphology **29**: 381–387. 1979.
- . Autonomous development of embryo in *Paspalum conjugatum* Berg. Bot. Not. **133**: 215–222. 1980. [$2n = 40$; asynaptic; apomictic and pseudogamous.]
- CHASE, A. The North American species of *Paspalum*. Contr. U.S. Natl. Herb. **28**: 1–310. 1929. [The most comprehensive monograph available for North American species.]

- CHRISTOPHER, J., P. S. RAJ, & K. G. PILLAI. Cytomorphological studies of three species of *Paspalum* Linn. from South India. *Cytologia* **52**: 487-491. 1987. [*P. scrobiculatum*, *P. orbiculare*, *P. Commersonii*.]
- CLAYTON, W. D. The *Paspalum scrobiculatum* complex in tropical Africa. *Kew Bull.* **30**: 101-105. 1975.
- CRINS, W. J., P. D. PRATT, & D. F. BRUNTON. *Paspalum ciliatifolium*, a grass new to Canada from southwestern Ontario. *Canad. Field Nat.* **91**: 422-424. 1977.
- DE WET, J. M. J., K. E. P. RAO, M. H. MENGESHA, & D. E. BRINK. Diversity in kodo millet, *Paspalum scrobiculatum*. *Econ. Bot.* **37**: 159-163. 1983.
- DUVAL-JOUE, M. J. Sur les parois cellulaires du *Panicum vaginatum* Godr. et Gren. *Bull. Soc. Bot. France* **16**: 110-114. 1869. [Aerenchyma in the rhizome of *Paspalum vaginatum* Swartz.]
- ELLIS, R. P. Comparative leaf anatomy of *Paspalum paspalodes* and *P. vaginatum*. *Bothalia* **11**: 235-241. 1974. [*P. paspalodes* (= *P. distichum*); species separable on basis of distribution of sclerenchyma, shape and thickness of leaf margin, shape of adaxial ribs and furrows and associated papillae.]
- FANG, J. S., & H. W. LI. Cytological study in *Paspalum conjugatum* Berg. *Bot. Bull. Acad. Sinica* **11**: 1-12. 1966. [$2n = 40$; asynaptic.]
- FERNANDES DE M., M. I. B., I. L. BARRETO, & F. M. SALZANO. Cytogenetic, ecologic and morphologic studies in Brazilian forms of *Paspalum dilatatum*. *Canad. Jour. Genet. Cytol.* **10**: 131-138. 1968.
- FORBES, I., & G. W. BURTON. Cytology of diploids, natural and induced tetraploids, and intraspecies hybrids of bahiagrass, *Paspalum notatum* Flügge. *Crop Sci. Madison* **1**: 402-406. 1961.
- FOURNIER, E. Sur un fait de dimorphisme dans la famille des Graminées. *Compt. Rend. Acad. Sci. Paris* **80**: 440, 441. 1875. [*Dimorphostachys* gen. nov. intermediate between *Paspalum* and *Panicum*.]
- GUÉDÈS, M. The case for *Paspalum distichum* and against futile name-changes. *Taxon* **25**: 512, 513. 1976.
- GUPTA, P. K., & A. K. SRIVASTAVA. Aberrant meiosis and spindle abnormalities in *Paspalum paspalodes* (Michx.) Scribn. (Gramineae). *Genetica* **43**: 76-83. 1972. [= *P. distichum*.]
- HANNA, W. W., & G. W. BURTON. Cytogenetics and breeding behavior of an apomictic hybrid in bahiagrass. *Jour. Hered.* **77**: 457-459. 1986.
- HODGSON, H. J. Flowering habits and pollen dispersal in Pensacola bahia grass, *Paspalum notatum*, Flügge. *Agron. Jour.* **41**: 337-343. 1949a. [Self-sterile.]
- . Effect of heat and acid scarification on germination of seed of bahia grass, *Paspalum notatum*, Flügge. *Ibid.* 531-533. 1949b. [Heat or acid will break dormancy.]
- HSIAO, A. I., & W. Z. HUANG. Apical dominance in the shoot and its possible role in the survival of *Paspalum distichum*. *Weed Res.* **29**: 327-334. 1989a.
- & ———. Effects of flooding on rooting and sprouting of isolated stem segments and on plant growth of *Paspalum distichum* L. *Weed Res.* **29**: 335-344. 1989b.
- ILIJANIC, L., & J. TOPIC. *Paspalum dilatatum* Poirét, a new adventitious plant in the flora of Yugoslavia. *Acta Bot. Croat.* **45**: 141-144. 1986.
- JOVET, P., & M. GUÉDÈS. *Paspalum distichum* L. and *P. paspalodes* (Michx.) Scribn. *Taxon* **21**: 546. 1972.
- KARR, J. R. An association between a grass (*Paspalum virgatum*) and moths. *Biotropica* **8**: 284, 285. 1976.
- KNIGHT, W. E. The influence of photoperiod and temperature on growth, flowering, and seed production of Dallisgrass, *Paspalum dilatatum* Poir. *Agron. Jour.* **47**: 555-559. 1955.

- LE COMTE, J. Monographie des espèces du genre *Paspalum* existantes dans les États-Unis d'Amérique. Jour. Physique **91**: 283-286. 1820. [Eighteen spp.; first monograph of North American species.]
- LOXTON, A. E. The taxonomy of *Paspalum paspalodes* and *P. vaginatum* as represented in South Africa. Bothalia **11**: 243-245. 1974. [Photographs of spikelets; *P. paspalodes* = *P. distichum*, which however, he rejects as a nomen confusum, but see GUÉDÈS (1976).]
- MURLEY, M. *Paspalum* in Iowa. Proc. Iowa Acad. Sci. **51**: 237-239. 1944. [Only *P. ciliatifolium* var. *stramineum* (= *P. setaceum* var. *stramineum*).]
- NARAYANASWAMI, S. The structure and development of the caryopsis in some Indian millets. III. *Paspalum scrobiculatum* L. Bull. Torrey Bot. Club **81**: 288-299. 1954.
- NEES AB ESENBECK, C. G. Agrostologia brasiliensis. ii + 608 pp. Stuttgart & Tübingen. 1829.
- NORMANN, G. A., C. L. QUARIN, & B. L. BURSON. Cytogenetics and reproductive behavior of different chromosome races in six *Paspalum* species. Jour. Hered. **80**: 24-28. 1989.
- PI, P.-H., & C.-Y. CHAO. Microsporogenesis in *Paspalum longifolium* and *P. Commersonii* on two different polyploid levels. Cytologia **39**: 453-465. 1974. [*P. longifolium* Roxb., natural tetraploid ($2n = 40$) induced, desynaptic octoploid ($2n = 80$) with restored synapsis; *P. Commersonii*, natural hexaploid ($2n = 60$) natural, asynaptic dodecaploid ($2n = 120$) with restored synapsis, induced dodecaploid still asynaptic.]
- PILGER, R. Bemerkungen zur Systematik der Gattung *Paspalum* L. Repert. Spec. Nov. **26**: 228-231. 1929. [Sectional classification.]
- PITMAN, M. W., B. L. BURSON, & E. C. BASHAW. Phylogenetic relationships among *Paspalum* species with different base chromosome numbers. Bot. Gaz. **148**: 130-135. 1987.
- POHL, R. W., L. H. TIFFANY, & J. R. KARR. Probable source of fluid from spikelets of *Paspalum virgatum* L. (Gramineae). Biotropica **11**: 42. 1979. [Fungal origin.]
- POWELL, J. B. Karyological leaf squashes in grasses, aided by pectinase digestion at 45°C. Stain Technol. **43**: 135-138. 1968. [Methodology; *P. notatum* the test organism; $2n = 40$.]
- PRITCHARD, A. J. The cytology and reproduction of *Paspalum yaguaronense* (Henr.). Austral. Jour. Agr. Res. **13**: 206-211. 1962.
- QUARIN, C. L., & B. L. BURSON. Cytogenetic relations among *Paspalum notatum* var. *Saurae*, *P. pumilum*, *P. indecorum*, and *P. vaginatum*. Bot. Gaz. **144**: 433-438. 1983.
- & W. W. HANNA. Effect of three ploidy levels on meiosis and mode of reproduction in *Paspalum hexastachyum*. Crop Sci. Madison **20**: 69-75. 1980.
- , ——— & A. FERNÁNDEZ. Genetic studies in diploid and tetraploid *Paspalum* species. Embryo sac development, chromosome behavior, and fertility in *P. cromyorrhizon*, *P. laxum*, and *P. proliferum*. Jour. Hered. **73**: 254-256. 1982.
- SAURA, F. Cariología de Gramíneas. Géneros *Paspalum*, *Stipa*, *Poa*, *Andropogon* y *Phalaris*. Revista Fac. Agron. Vet. Univ. Buenos Aires **10**: 344-353. 1943. [Chromosome numbers, three species of *Paspalum*.]
- . Cariología de Gramíneas en Argentina. Ibid. **12**: 51-67. 1948. [Chromosome counts, observations on meiosis, pollen fertility assessments for ten species of *Paspalum*.]
- SMITH, B. W. Hybridity and apomixis in the perennial grass, *Paspalum dilatatum*. (Abstr.) Genetics **33**: 628, 629. 1948.
- SNYDER, L. A. Apomixis in *Paspalum secans*. Am. Jour. Bot. **44**: 318-324. 1957.
- . Asyndesis and meiotic non-reduction in microsporogenesis of apomictic *Paspalum secans*. Cytologia **26**: 50-61. 1961. [Obligately apomictic, pseudogamous.]

VASEY, G. Notes on the Paspali of Le Comte's monograph. Proc. Acad. Sci. Phila. **38**: 284-290. 1886.

WILLEMOËS, J. G., J. BELTRANO, & E. R. MONTALDI. Diagravitropic growth promoted by high sucrose contents in *Paspalum vaginatum*, and its reversion by gibberellic acid. Canad. Jour. Bot. **66**: 2035-2037. 1988.

17. *Reimarochloa* Hitchcock, Contr. U.S. Natl. Herb. **12**: 198. 1909.

Decumbent [stoloniferous, caespitose] perennials. Stems with glabrous nodes; internodes hollow [solid]. Leaves basally aggregated or cauline, distinctly distichous or not; sheaths pubescent [glabrous]; ligule a membrane [fringe of hairs]; blades linear, flat, folded or involute, glabrous to pubescent, with attenuate to truncate bases; photosynthesis C_4 , biochemical pathway NADP-me. Inflorescences panicleate, of 1-4 [6] subdigitate or racemose spike-like primary branches that disarticulate as units; rachides flattened; branches terminating in spikelets or in naked points. Spikelets lanceolate, dorsiventrally compressed, planoconvex, abaxial, secund, subsessile (the inconspicuous pedicel apices truncate), solitary, biseriate; proximal florets sterile, epaleate. Calli undifferentiated. Glumes absent (distal glume rarely present). Proximal lemmas equalling and similar in texture or less firm than distal lemmas, glabrous, awnless, 3 nerved; distal lemmas chartaceous, striate (smooth), glabrous, acuminate, awnless, 3 nerved, with involute margins and conspicuous germination flap. Distal paleas gaping, awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas red to brown. Caryopses (grains) small, smooth; pericarp thin. Base chromosome number 9. TYPE SPECIES: *Reimarochloa acuta* (Flüggé) Hitchc. (Named for J. A. H. Reimar, a medical doctor and professor of natural history in Hamburg, Germany, combined with Greek, *chloë*, grass). — REIMARGRASS.

A poorly known genus of four species of moist shores, ditches, and disturbed ground, from Florida through the West Indies, Central America, and northern South America to Argentina. The genus was excised from *Reimaria* Flüggé by Hitchcock (1909). *Reimaria* was a mixture of three elements, two of which are species of *Paspalum*, and one of which is a *Reimarochloa* Hitchc. *Paspalum* is almost certainly the closest relative of *Reimarochloa*.

Reimarochloa is the only genus of the Paniceae in the Southeast that lacks glumes. It also differs from *Paspalum* in having a point of disarticulation at the base of the primary inflorescence branches, two stamens, and papery distal lemmas. It also tends to have more acuminate spikelets. These characters also distinguish *Reimarochloa* from *Axonopus* Beauv., although these genera also differ in spikelet orientation (abaxial vs. adaxial, respectively). Clayton & Renvoize note that it superficially resembles *Digitaria* but that its true relationship is with *Paspalum*.

A single species, *Reimarochloa oligostachya* (Munro) Hitchc., Florida reimargrass, occurs in our region, in central Florida.

Some species of *Reimarochloa* have prominent spikelet hairs that may assist in adhesion or dispersal by wind (Davidse, 1987). However, disarticulation of the inflorescence branches as units argues against this dispersal mechanism, unless secondary disarticulation of the spikelets occurs.

REFERENCES:

Under references for tribe see CHASE (1911); CLAYTON & RENVOIZE; DAVIDSE (1987); HITCHCOCK (1909); and WEBSTER (1988).

18. *Axonopus* Palisot de Beauvois, Essai Agrost. 12. 1812.

Stoloniferous or caespitose perennials (annuals). Stems 15–100 [300] cm high, flattened laterally (in some species); internodes solid or spongy; nodes glabrous (pubescent). Leaves with sheaths glabrous or pubescent; ligule a fringed membrane [fringe of hairs]; blades linear or lanceolate to ovate, flat or folded, glabrous or pubescent, margins often ciliate, obtuse or rounded at apex, truncate to rounded at base, rolled in bud; photosynthesis C_4 , biochemical pathway NADP-me. Inflorescences of 2–4 [–many] spike-like, digitate or subdigitate to racemose primary branches; rachides 3-angled, winged, smooth or scabrous, terminating in spikelets. Spikelets oblong-elliptic, dorsiventrally compressed, disarticulating below the glume, adaxial, secund, short-pedicellate (pedicel apices truncate or discoid), solitary, biseriate; proximal florets sterile, epaleate. Calli undifferentiated. Glumes 1, equal to proximal lemmas, glabrous or pubescent, acute to acuminate (obtuse), awnless, 0–9 nerved, midrib often poorly developed. Proximal lemmas slightly longer and less firm than distal lemmas, glabrous or pubescent, acute to acuminate (obtuse), awnless, 0–2 nerved; distal lemmas cartilaginous, glabrous, smooth, brown or yellow, lustrous or dull, awnless, 4 nerved, with involute (or in *A. fastigiatus* flat) margins and conspicuous germination flap. Distal paleas indurate [not indurate]. Lodicules 2. Ovaries with styles free, stigmas red or brown. Caryopses (grains) small, smooth. Base chromosome number 10.¹⁸ LECTOTYPE SPECIES: *Axonopus compressus* (Sw.) Beauv.; see Chase, Proc. Biol. Soc. Wash. 24: 129. 1911. (Name from Greek, *axon*, axle or axis, and *pous*, foot.) — CARPETGRASS, IMPERIAL GRASS.

A largely Neotropical genus containing approximately 110 species of wetlands or moist to dry woodlands, disturbed areas, lawns, and cultivated fields. One species, *Axonopus brevipedunculatus* Gledhill, is endemic to Africa. Two species, *A. affinis* Chase and *A. compressus*, have been introduced throughout the tropics as lawn and pasture grasses. They may become weedy on fertile soils, and *A. compressus* has

¹⁸Since the base chromosome number of *Axonopus* is 10, reports of $2n = 54$ for *A. affinis* (Brown, 1946) and $2n = 56$ for *A. compressus* (Nuñez in Parodi, 1946) are probably in error.

been known to take over pastures of *Paspalum dilatatum*, a superior forage species (McLennan). However, *A. compressus* can grow on land of low fertility where *P. dilatatum* does poorly.

Three sections are recognized within *Axonopus*: sect. *AXONOPUS* (rachis and spikelets glabrous to pubescent), sect. *CABRERA* (Lag.) Chase (rachis with stiff, golden, tubercle-based hairs), and sect. *LAPPAGOPSIS* (Steudel) Chase (spikelets with stiff, white, tubercle-based hairs). The three species of the Southeast are in sect. *AXONOPUS* series *Axonopus* (usually stoloniferous, stems less than 1 m tall, leaf apices obtuse or acute, racemes generally less than 10, glumes with suppressed midnerve) (Black). *Axonopus affinis*, common carpetgrass, $n = 10, 20, 40$, and *A. compressus*, tropical carpetgrass, $n = 20, 30, 40, 49, 50$, are closely related. The former has narrower and shorter spikelets, generally narrower leaves, and nodes and leaf surfaces that are glabrous or nearly so, whereas *A. compressus* has larger spikelets, broader leaves, and pubescent nodes and leaf surfaces. *Axonopus affinis* occurs from Virginia and Arkansas south throughout our area, and west to Oklahoma and Texas. It has been introduced into Hawaii, the Philippines, Singapore, and Australia. *Axonopus compressus* has a somewhat more southern distribution in the United States, extending from South Carolina south to Florida and west to Texas. It is distributed southward through Central America and the Antilles to southern Brazil, Uruguay, Bolivia, and Peru. It is widely naturalized in Africa, southeastern Asia, the Pacific region, and Australia. An aneuploid race has been detected in Costa Rica ($10x-1$; Davidse & Pohl, 1972). *Axonopus furcatus* (Flüggé) Hitchc., big carpetgrass, $n = 20$, differs from both of those species in having entirely glabrous, larger spikelets. It occurs mainly on the Atlantic and Gulf Coastal Plain, from Virginia to Texas, and inland to Arkansas, and is also found in Cuba.

Axonopus is very similar to *Paspalum*, the two differing only in the orientation of the spikelets relative to the rachis (adaxial in *Axonopus*, abaxial in *Paspalum*). Palisot de Beauvois noted this close relationship when he described *Axonopus*, and some authors (e.g., Hackel) have considered *Axonopus* and its segregates to be sections of *Paspalum*. The base chromosome numbers of *Axonopus* and *Paspalum* are also identical. *Axonopus* is also superficially similar to *Digitaria* but differs in its adaxial spikelets and the presence of solitary (rather than paired) spikelets at each node along the rachis (Pohl, 1980). Watson & Dallwitz's nearest-neighbor analysis suggests that *Brachiaria sensu lato* (now mostly *Urochloa*), *Paspalum*, *Panicum*, and *Urochloa* are similar phenetically. Butzin (1970) placed *Axonopus* with *Brachiaria*, *Eriochloa*, and *Reimaria* (= *Reimarochloa* pro parte) in subtribe Brachiariinae, and Shaw & Smeins (1979) noted similarities between *Axonopus* and *Eriochloa* in the pedicel apex and disarticulation point of the spikelet. Black concluded that *Axonopus* stood apart from all other genera of the Paniceae, but this is untenable, given the minor differences noted above.

The center of diversity, and perhaps the center of origin, for *Aronopus* is in central Brazil (Hickenbick *et al.*). It has also been suggested that *Aronopus* ser. *Aronopus* is the oldest (most primitive?) group of taxa in the genus, but the evidence for this hypothesis is obscure (Hickenbick *et al.*).

Natural hybrids can form among species of different series, suggesting that the series are not well differentiated. Reticulate evolution, therefore, may have been important in the diversification of this genus. Hickenbick and coworkers suggested that allopolyploidy was important in the diversification of species in series *Aronopus* and *Suffulti* G. A. Black. In ser. *Suffulti*, hybridization has involved subspecies rather than species. In such cases the allopolyploids are segmental. In ser. *Aronopus* few multiple associations of chromosomes are seen, even though polyploidy up to the decaploid ($10x$) level is known. These may involve polyploidization of intraspecific hybrids with concurrent selection for the establishment of regular meiosis (Hickenbick *et al.*).

The reproductive biology of species of *Aronopus* has not been well studied. In *A. fissifolius* (Raddi) Kuhl., of Argentina, increases in lodicule volume cause the floret to open during anthesis (Anton). After fertilization, the lodicules diminish in volume. The flowers are chasmogamous, and both cross- and self-pollination may occur, although nothing is known about incompatibility systems in the genus. Apomixis is known in *A. brevipedunculatus* and *A. arenosus* Gledhill, in which fruit may set in unopened spikelets (Gledhill). In single clones of *A. brevipedunculatus* a great deal of phenotypic plasticity can be exhibited under different environmental conditions. Morphological variability is also evident in sexual species such as *A. affinis* and *A. flexuosus* (Peter) C. E. Hubb. ex Troupin (Gledhill). *Aronopus affinis* flowers mainly in the late summer (July-August) in the Southeast, as do many panicoids. It undergoes a period of dormancy (no growth) from late November to early February (Patton & Judd).

REFERENCES:

- Under references for tribe see BLOMQUIST; BOLKHOVSKIKH *et al.*; BROWN (1946); BUTZIN (1970); CHASE (1911); CHIPPINDALL; CLAYTON & RENOIZE; CLEWELL; DAVIDSE & POHL (1972a, b, 1974); GOULD (1975, 1979); HACKEL; JONES & COILE; MACROBERTS; PALISOT DE BEAUVOIS; PATTON & JUDD; POHL (1980); RADFORD *et al.*; E. SMITH; WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.
- ANTON, A. M. Estudios sobre la biología reproductiva de *Aronopus fissifolius* (Poaceae). Bol. Soc. Argent. Bot. **21**: 81-130. 1982.
- BLACK, G. A. Grasses of the genus *Aronopus* (a taxonomic treatment). Adv. Front. Pl. Sci. **5**: 1-186. 1963. [Posthumous; infrageneric classification presented.]
- BLASER, R. E., & W. E. STOKES. The chemical composition, growth, and certain deficiency symptoms of carpetgrass, *Aronopus affinis*, as affected by lime and fertilizer mixtures. Jour. Am. Soc. Agron. **34**: 765-768. 1942. [*A. affinis* thrives on poor soils; its growth enhanced by adding nutrients.]
- CROSS, D. O. Narrow-leaved carpet grass. Agr. Gaz. New S. Wales **49**: 647. 1938. [Spikelets of *A. compressus* and *A. affinis* illustrated.]

- DAVIDSE, G. Four new species of *Axonopus* (Poaceae: Paniceae) from tropical America. *Ann. Missouri Bot. Gard.* **74**: 416–423. 1987. [Distinguishing features of *Axonopus* listed.]
- GLEDHILL, D. Cytotaxonomic revision of the *Axonopus compressus* (Sw.) Beauv. complex. *Bol. Soc. Brot.* **II**. **40**: 125–147. 1966. [Good experimental data on phenotypic plasticity.]
- HENRARD, J. T. Some new species of *Axonopus* (Gramineae). *Blumea* **5**: 274–279. 1942. [Characters useful in the taxonomy of *Axonopus* differ from those in *Digitaria*; vegetative characters important in *Axonopus*.]
- . On a new species of *Axonopus* from South America, with critical observations. *Ibid.* **5**: 525–529. 1945.
- HICKENBICK, M. C. M., J. F. M. VALLS, F. M. SALZANO, & M. I. B. DE MORAES FERNANDES. Cytogenetic and evolutionary relationships in the genus *Axonopus* (Gramineae). *Cytologia* **40**: 185–204. 1975.
- JAGOE, R. B. Carpet grass, *Axonopus* spp. *Gard. Bull. Straits Settl.* **11**: 109–118. 1940. [Differences between *A. compressus* and *A. affinis*.]
- MCLENNAN, L. W. Carpet grass. Has it a place in north coast pastures? *Agr. Gaz. New S. Wales* **47**: 555–558, 601. 1936. [Yes, on poor soils.]
- REYES, C. R. Gramíneas de la Mesa de Cavacas: El género *Axonopus*. *BioLlania* **4**: 21–28. 1985. [Four spp.]
- SCHOLZ, H. Notizen zu einigen *Axonopus*-Arten (Gramineae-Paniceae), nach Berliner Typenmaterial. *Willdenowia* **8**: 93–99. 1977. [Two species of *Paspalum* treated under *A. compressus*; many nomenclatural notes for non-North American species.]
- SHAW, R. B., & F. E. SMEINS. Epidermal characteristics of the callus in *Eriochloa* (Poaceae). *Am. Jour. Bot.* **66**: 907–913. 1979. [Pedicel apex and disarticulation point of spikelet similar to *Axonopus*.]

19. *Setaria* Palisot de Beauvois, *Essai Agrost.* 51, 178. 1812, nom. cons.¹⁹

Rhizomatous, decumbent, or caespitose [stoloniterous], perennials or annuals. Stems 15–400 cm high; internodes solid to hollow; nodes glabrous or pubescent. Leaves with sheaths glabrous or pubescent; ligule a fringed membrane or a fringe of hairs; blades linear to lanceolate, flat or folded, glabrous to pubescent, with truncate, rounded, or sagittate bases, pseudopetiolate or not, rolled, folded, or plicate in bud; photosynthesis C₄, biochemical pathway NADP-me. Inflorescences paniculate, often greatly contracted, ovoid, spike-like or more open, primary branches often spike-like or further reduced and the spikelets appearing fasciculate, axes terminating in bristles. Spikelets dorsiventrally compressed, planoconvex to terete, disarticulating below the glumes (or below distal lemma in some cultivated taxa), abaxial, secund [or not], pedicellate (pedicel apices discoid), solitary, some or all subtended by 1–many yellow, green, or purple, scabrous bristles (greatly reduced branches); proximal florets staminate or sterile, paleate or epaleate.

¹⁹Although debate over the use of the name *Setaria* was resolved by conservation, a body of literature about its application accumulated at the turn of the century. The strongest arguments in favor of its present usage, with *Setaria viridis* (L.) Beauv. as its type, were put forward by Stapf (1920). A dissenting view was expressed by Hitchcock (1920).

Calli undifferentiated. Glumes 2, unequal, awnless; proximal glumes grooved or smooth, acute to mucronate, 3–5 nerved, encircling spikelet base; distal glumes shorter than to equalling distal lemmas, 3–9 nerved. Proximal lemmas equalling or exceeding and less firm than distal lemmas, smooth or with median groove, awnless, 5–7 nerved; distal lemmas cartilaginous, transversely rugose (smooth in *S. magna*), glabrous, acute, awnless, 1–5 nerved, with involute margins and conspicuous germination flap. Distal paleas indurate, awnless, 2 nerved. Lodicules 2. Ovaries with styles free, stigmas white or red. Caryopses (grains) small, not grooved, sculptured or smooth; endosperm hard, without lipid, containing simple starch grains. Base chromosome number 9. (Including *Chaetochloa* Scribner.) LECTOTYPE SPECIES: *Setaria viridis* (L.) Beauv., typ. cons.; see ICBN 1989. (Name from Latin, *setum*, bristle, and suffix *-arius*, possessing, in reference to the bristles subtending the spikelets.) — FOXTAIL, FOXTAIL MILLET, BRISTLEGRASS.

A genus of about 100 species, mostly of tropical and subtropical regions, but with several species occurring in the cooler parts of both Northern and Southern hemispheres, mainly as weeds of crops. Species of *Setaria* occur in a wide array of habitats, including dry open woodlands, beaches, wet open areas, disturbed areas, and cultivated fields. Three subgenera are currently recognized. Five indigenous and ten introduced species have been recorded from the Southeast.

Subgenus PTYCHOPHYLLUM (A. Br.) Rominger (perennial or annual, leaves plicate, often pseudopetiolate, some but not all spikelets subtended by one to several bristles, bracts of distal florets transversely rugose or nearly smooth) contains six species in North and Central America (Rominger). This subgenus appears to be natural. However, ten species from subgenera *Ptychophyllum* and *Setaria* analyzed by cluster analysis showed no clear separation along subgeneric lines (Chikara & Gupta). This result should be interpreted cautiously, however, because such analyses are dependent on the characters chosen. Moreover, cluster analysis groups individuals on the basis of overall similarity, not phylogenetic divergence. Two species of subg. *Ptychophyllum* occur in the Southeast. *Setaria barbata* (Lam.) Kunth, Mary grass, corn grass, $n = 27$, $2n = 54$, 56, (annual, panicles narrow, spikelets 2.2–2.7 mm long, bristles 3–11 mm long) has been collected on ballast in Florida (Hall, Rominger). *Setaria palmifolia* (Koenig) Stapf, palmgrass, $n = 27$, (perennial, panicles diffuse, spikelets 3–3.3 mm long, bristles 1–9 mm long), has escaped from cultivation into disturbed woods and swamps in Florida and Louisiana (Clewett; MacRoberts; Wunderlin). It is a forest grass native to Asia (Bor, 1954).

Subgenus PAUROCHAETIUM (Hitchc. & Chase) Rominger (*Panicum* subg. *Paurochaetium* Hitchc. & Chase) (perennials, leaves flat, not pseudopetiolate, uppermost spikelet of each branchlet subtended by only a single bristle, distal floret bracts finely rugose) contains ten species in North America. This group is questionably natural (Rominger). *Setaria Chapmanii* (Vasey) Pilger (*Panicum Chapmanii* Vasey) is

the only member of the subgenus in the Southeast. Its center of distribution is in the Florida Keys, and it is restricted to soils derived from coral and shells (Rominger). Several other species of this subgenus occur in Texas (e.g., *S. firmula* (Hitchc. & Chase) Pilger, *S. ramiseta* (Scribner) Pilger, *S. Reverchonii* (Vasey) Pilger; Rominger).

Subgenus *SETARIA* (perennials or annuals, leaf blades flat, not pseudopetiolate, all spikelets subtended by one to several bristles, bracts of distal florets coarsely or finely rugose, rarely smooth) is the largest of the three subgenera. Several of its representatives in our area are native. *Setaria corrugata* (Ell.) Schultes, coastal foxtail, (annual, nodes pubescent, panicles cylindrical, spikelets 1.8–2 mm long, distal lemmas coarsely rugose, bristles highly variable in length and color, 2.5–20 mm long and green, orange or purple), described from material collected in Georgia, occurs along the Atlantic and Gulf Coastal Plain from North Carolina to Florida and eastern Texas. It superficially resembles the introduced *S. viridis* (L.) Beauv. (see below). It grows on sandy soils in pine and oak woods but has also spread to open cultivated fields, waste places, and clearings (Hall; Lelong, 1988; Rominger). *Setaria geniculata* (Lam.) Beauv., knotroot foxtail, knotroot bristlegrass, $n = 18, 36$, (perennial, rhizomes short and knotted, nodes glabrous, panicle cylindrical, dense, spikelets 2–2.5 mm long, distal lemmas finely rugose, bristles 5–10 below each spikelet, yellow to purple) is widespread in North America, occurring from Massachusetts to Florida, and along the Gulf Coast to Texas. Blomquist noted that, at least in North Carolina, it was most common on the Coastal Plain. It also occurs inland to Arkansas and Kansas and is known from every state in our area. It occupies dry and wet, open habitats, including fresh and brackish marshes, swales, ditches, prairies, woodland clearings, and fields. *Setaria macrosperma* (Scribner & Merr.) K. Schum., coral foxtail, (perennial, nodes glabrous, panicles open but with branches less than 8 cm long, spikelets 2.7–3.1 mm long, distal lemmas finely rugose, bristles 4–30 mm long) occurs in Florida, coastal Georgia, and South Carolina, on coral soils and shell mounds, and sometimes also in old fields or in hammocks (Hall, Radford *et al.*, Rominger, Wunderlin). *Setaria magna* Griseb., giant bristlegrass, giant millet, cattail millet (annual, nodes glabrous, panicles cylindrical to somewhat open, up to 58 cm long, spikelets 1.9–2.4 mm long, distal lemmas smooth, brown, lustrous, bristles 1 or 2 below each spikelet, 0.5–2 cm long), the most robust of the North American species of *Setaria* (stems to 4 m tall), is native to brackish marshes from New Jersey to Florida, and along the Gulf Coast to eastern Texas. It is also known from saline marshes in Arkansas (Gould, 1975; Rominger; E. Smith).

A series of introduced weeds and a closely related crop plant are also members of subg. *SETARIA*.

Setaria adhaerans (Forskål) Chiov., $2n = 18$, (annual, nodes glabrous, panicles cylindrical, spikelets 1.5–2 mm long, distal lemmas finely rugose) is a tropical species that has appeared spontaneously on ballast in Alabama, Louisiana, and Texas. It is similar to *S. verticillata* (L.)

Beauv., hooked bristlegrass, $n = 18$, $2n = 18$, 36 , (annual, nodes glabrous, panicle cylindrical, spikelets 1.9–2.2 mm long, distal lemmas finely rugose, bristles usually 1 or 2 below each spikelet, green to pale yellow-brown, retrorsely scabrous, or antrorsely scabrous in var. *ambigua* (Guss.) Parl.), which appears to be a recent adventive in the Southeast. Rominger reported in 1962 that no records of the typical variety were known in our area, but that var. *ambigua* had been recorded in Alabama. However, by 1978, Hall indicated that *S. verticillata* (varieties not distinguished) was infrequent in cultivated fields in southern Florida, and Wunderlin noted it as rare in central Florida. It is very widespread farther north from Vermont to British Columbia and south to Virginia, Oklahoma, and California (Rominger; Steel *et al.*).

Setaria Faberi W. Herrm., giant foxtail, Chinese foxtail, nodding foxtail, $n = 18$, (annual, nodes glabrous, panicle cylindrical, large and often drooping, spikelets 2.5–3 mm long, distal lemmas finely rugose, bristles 1–3 below each spikelet, 0.8–1.3 mm long) is becoming increasingly widespread in our region (Blomquist; Duncan; Fairbrothers, 1959; Jones & Coile; Lelong, 1988; MacRoberts; Rominger; E. Smith; Wood). It is a very common weed of disturbed soils, cultivated fields, and railway sidings and roadsides in the Northeast and in the southern parts of Ontario and Quebec. It has often been confused with a close relative, *S. viridis*, green foxtail, green bristlegrass, pigeon millet, $n = 9$, $2n = 36$, (annual, nodes glabrous, panicle cylindrical, usually quite straight, spikelets 1.8–2.5 mm long, distal lemmas finely rugose, bristles 1–3 below each spikelet, green to purple), which is often sympatric with it in cultivated fields and other disturbed areas. In *Setaria Faberi* the upper leaf surface is strigose, while in *S. viridis* it is glabrous or glabrate.

Setaria viridis (glabrous or scabrous leaf surfaces) has become naturalized in almost all parts of North America except the Arctic and the warmest parts of our region in Florida. Another member of the *S. viridis* complex is *S. viridis* subsp. *italica* (L.) Briq. (often called *S. italica* (L.) Beauv.), Italian millet, foxtail millet, German millet, Hungarian grass, $n = 9$, (annual, nodes finely pubescent, panicle cylindrical, dense, often lobed, spikelets 2–2.5 mm long, distal lemmas finely rugose, bristles 2 or 3 below each spikelet, green to purple). It differs from *S. viridis* subsp. *viridis* mainly in its longer panicles (8.5–26.5 cm vs. 1–6 cm) and the site of disarticulation, which is between the glumes and proximal lemma in subsp. *italica* and below the glumes in subsp. *viridis*. Subspecies *italica* is planted for forage and grain and has escaped from cultivation sparingly from northern Florida northward and westward. Due to the selection for agronomic features, its patterns of morphological variation are complex, involving, for example, fruit color, bristle color and length, and panicle density and lobing. Hubbard produced a taxonomic scheme to account for all of this variation, but the taxa in his scheme are probably not genetically stable.

Setaria glauca (L.) Beauv. (*S. lutescens* (Wieg.) F. T. Hubb., *S. pumila* (Poir.) Roemer & Schultes, *Pennisetum glaucum* (L.) R.

Br.), yellow foxtail, yellow bristlegrass, $n = 18$, $2n = 72$, (annual, nodes glabrous, panicle cylindrical, dense, spikelets 3 mm long, distal lemmas finely rugose, bristles 5–14 below each spikelet, yellow) is very much like *S. viridis* in distribution and habitat preferences and, like it, was introduced from Eurasia. Considerable effort has been expended on determining the application of the epithet "glauca." The most detailed treatment was presented by Terrell, who concluded that the epithet belongs to *S. glauca*, and that pearl millet must properly be called *Pennisetum americanum* (L.) Leeke. Other discussions include those by Chase (1921), Clayton (1979), Hitchcock (1920), Hubbard, McNeill & Dore, Reeder (1951), and Stapf (1928).

Setaria pallidifusca (Schum.) Stapf & C. E. Hubb. (annual, nodes glabrous, panicles cylindrical, spikelets 2–2.5 mm long, distal lemmas coarsely rugose, bristles five below each spikelet, yellowish), an African species, has been reported from several locations in southern Louisiana (MacRoberts).

Setaria setosa (Sw.) Beauv. (including *S. rariflora* Mikan ex Trin.; Renvoize) (annuals or short-lived perennials, panicles cylindrical, slender, interrupted, spikelets 2 mm long, distal lemmas finely rugose, bristles 1 or 2 below each spikelet) is also a rare adventive in our area, found on ballast in Florida and Alabama (Rominger).

Most authors agree that *Setaria* is related to *Panicum*. These genera are placed in the same subtribe, but the degree of relationship is uncertain. *Setaria* has some, and often many, branches that are reduced to bristles (Beal; Butzin, 1977; Narayanaswami, 1956; Sohns, 1954), and it also has rugose distal lemmas and paleas. These features suggest relationships with *Paspalidium*, *Urochloa*, and *Eriochloa* (Blake). *Setaria* has the most characters in common with *Paspalidium* (e.g., bristles, rugose distal floret bracts, NADP-me decarboxylation pathway) (Brown, 1977; Gutierrez *et al.*; Hattersley, 1984; Prendergast & Hattersley). Clayton & Renvoize and Webster (1987) agree with this assessment. *Paspalidium* is also most similar to *Setaria* in the phenetic analysis of Watson & Dallwitz. Other genera in order of decreasing similarity in their analysis include *Cymbosetaria* Schweik. (lumped with *Setaria*; Clayton & Renvoize), *Panicum*, and *Echinochloa*. An alternative view (Pohl, 1980) has *Pennisetum* as a close relative (both have bristles below the spikelets). However, this feature is more likely a parallelism, developed in two divergent lineages (*Pennisetum* is in subtribe Cenchrinae).

Relationships within the genus have not been assessed to any great extent. Rominger commented that subg. *Paurochaetium* might be polyphyletic. Ohwi described several series within sect. *Setariotypus* Ohwi (= subg. *Setaria* as treated here). However, the attention directed toward determining relationships within the genus has focused only on a few species complexes. One of these is the *Setaria viridis* complex. The behavior of hybrids produced between various taxa in the complex has been studied, partly with the aim of determining the origin of Italian millet. Natural and synthetic hybrids between *S. viridis*

subsp. *viridis* and subsp. *italica* have normal chromosome pairing at meiosis and fertility as great as both parents (De Wet *et al.*, 1979; Kihara & Kishimoto; Li *et al.*, 1945; Rao *et al.*, 1987) and contain the same genome (Li *et al.*, 1942). These authors consider typical *S. viridis* to be the progenitor of subsp. *italica*. Another member of the complex, *S. Faberi*, contains the A genome from *S. viridis*, as well as a non-homologous B genome, the source of which is unknown (Li *et al.*, 1942). Using cluster analysis, Williams & Schreiber examined morphological relationships in this complex and found that several robust cultivated varieties of *S. viridis* link most closely with *S. viridis* var. *major* (Gaudin) Posp., which, in turn, is closest to *S. viridis* subsp. *italica*, and then typical *S. viridis*. This group of *S. viridis* derivatives was then linked successively to *S. Faberi*, *S. verticillata*, and finally, *S. glauca*. Alcohol-soluble natural products provided a congruent estimate of phenetic relationship (Williams & Schreiber).

Polyploidy is prevalent in *Setaria*. *Setaria geniculata* contains tetraploid and octoploid races (Kishimoto; Sacchet & Boldrini), as does *S. glauca* (Björkqvist *et al.*; Javurková; Khosla & Singh; Kli-phuis; Malik & Tripathi; Shanthamma *et al.*). Within subg. *Setaria*, ploidy levels between diploid and octoploid are known in various species. Kishimoto noted a correlation between chromosome number and pollen diameter among various species. Emery (1957a) detected three chromosome races in *S. leucopila* (Scribner & Merr.) K. Schum. ($2n = 54, 68, 72$). Thus, in addition to the two eupolyploid races ($2n = 54, 72$), this species contains an aneuploid race. He also found that the hexaploid and aneuploid races were aposporous and pseudogamous but that the octoploid race had restored sexuality (Emery, 1957b). In the *S. macrostachya* Kunth complex (to which *S. leucopila* belongs) chromosome number races and varying reproductive strategies contribute to the complexity of phenotypic variability (Emery, 1957a, b).

Phenotypic variation in the *Setaria sphacelata* (Schum.) Stapf & C. E. Hubb. ex M. B. Moss complex has also caused taxonomic problems. The complex contains tetraploid to decaploid plants. Clayton (1966) initially recognized three species in the complex in West Africa but acknowledged that taxonomic problems still existed. Hacker's investigations (1966; 1968a, b) have shed more light on the situation. Autopolyploidy is believed to be responsible for the proliferation of ploidy levels, although the ancestor was probably an allotetraploid with two genomes (Hacker, 1968a). Hybrids were readily produced among several "species" in the complex, and plants of different ploidy levels showed high degrees of cross-compatibility. Also, within a ploidy level, there was almost complete homology between chromosomes of different "species." On the basis of the results of hybridization experiments and meiotic analyses, Hacker (1968b) doubted that any of the taxa in the complex warranted distinct specific status. In addition to the chromosomal homology among taxa, there is also no correlation between chromosome number and morphology (Hacker, 1966). Clayton (1979) concurred and reduced all of the segregates to varietal status.

On rare occasions aneuploids were found among the progeny in some of the crosses in the *Setaria sphacelata* complex (Hacker, 1968b), and as noted above, Emery (1957a) found an aneuploid race in *S. leucopila*. However, true aneuploidy appears to be rare in *Setaria*. A few instances of B chromosomes have also been reported, for example, in *S. glauca* (Khosla & Singh) and in the *S. sphacelata* complex, in which all chromosome races except the decaploids had at least one B chromosome (Hacker, 1966).

The mode of inheritance in a few character systems has been investigated in *Setaria*. An initial study of the inheritance of fruit characteristics in *S. viridis* subsp. *italica* showed that seed coat color is determined by three loci, endosperm features are controlled by two loci, and inflorescence form is controlled by two loci, while double inflorescences are not heritable (Li *et al.*, 1940). In hybridization experiments with *S. viridis* subsp. *viridis* and subsp. *italica*, 15 gene differences between these taxa were detected (Li *et al.*, 1945).

Niklas experimented on the aerodynamics of pollen flow around grass panicles, using *Setaria geniculata* as a model for compact panicle form. Pollen grains moving over the windward and lateral surfaces of the panicle tended to aggregate in an eddy on the leeward side, where they recirculated. The oscillations of the panicle in the air current thrust the panicle into the recirculating pollen. Thus, the panicle can capture pollen in this way, in addition to obtaining pollen that lands directly through sedimentation. He noted that there was a high probability that pollen produced by an inflorescence would be captured in the same inflorescence, an important consideration in self-compatible, annual weeds.

Studies of reproductive energy allocation in *Setaria Faberi*, *S. glauca*, *S. pallidifusca*, *S. x pycnocomma* (Steudel) W. Herrm., and *S. viridis* showed that all had very similar reproductive strategies, in spite of differences in size and ploidy level (Kawano & Miyake). All were predominantly inbreeding and allocated energy to reproductive output very efficiently, as may be typical of inbreeding annuals that grow in frequently disturbed, unpredictable habitats (Kawano & Miyake).

Setaria glauca contains two ecotypes in India. A long-panicled form grows in moist habitats. Its above-ground biomass is large, and it has a high reproductive capacity. The short-panicled form grows in dry sites and has a larger root system but produces fewer seeds (Ramakrishnan, 1963). There is no evidence, however, that these characteristics are genetically controlled. On the other hand, Schoner *et al.* have characterized a biotype from California that has a prostrate growth form and glaucous foliage. These features are stable under common garden conditions, as are the features of a biotype from eastern North America. The prostrate growth form appears to be selectively advantageous when it grows in alfalfa (*Medicago sativa* L.) fields.

One perennial species, *Setaria nigristrois* (Nees) Dur. & Schinz, is a major element of the latest stages of veld succession (Gibbs Russell, 1983). Little else seems to be known about the ecology of the perennials.

Setaria glauca has a germination inhibitor in the seed coat (Melkania). Dormancy lasts for approximately four months, but scarification can halt the dormancy (Ramakrishnan, 1963). Rost (1972) attempted to determine in finer detail the mechanism involved in breaking dormancy in this species. He found that digestion of protein bodies occurred in both dormant and nondormant embryos but that lipid content did not decrease in hydrated dormant embryos, while it did decrease in germinating ones. Thus, the breaking of dormancy must involve a process initiated at the time of germination rather than an ongoing process such as protein-body digestion. *Setaria Faberi* shows a bimodal pattern of seed germination. Seedling mortality occurs after both spring and late-summer germination episodes, but seedlings produced from later germinations tend to be more successful in terms of reproductive output, perhaps due to the senescence of competing winter annuals in the fields in which it occurs (Raynal & Bazzaz).

Limited attention has been paid to secondary metabolites in *Setaria*. Williams & Schreiber compared arrays of alcohol-soluble constituents in the *S. viridis* complex with patterns of morphological variation, but the compounds were not characterized. *Setaria glauca* contains a common C-glycosylflavone, isoorientin, and the flavone luteolin-7-O-rutinoside (Kaneta & Sugiyama). The most significant work is that of Gluchoff-Fiasson and coworkers, who have detected 40 flavonoids in *S. viridis* subsp. *italica* and characterized 22 of them. Among its flavonoid compounds are six flavone O-glycosides (based on apigenin, luteolin, chrysoeriol, and tricetin) and ten C-glycosides (xylosyl and glucosyl derivatives of vitexin, isoorientin, orientin, and soparin). Several of these C-glycosylflavones are not yet known from other natural sources.

The dispersal value of the bristles of *Setaria* must be questioned, since the spikelets disarticulate above the bristles. Davidse (1987) suggested the possibility that they may serve as a shaking mechanism, whereby mature spikelets would be dislodged when the bristles came into contact with fur or some other adhesive surface.

The few fossils of *Setaria* that have been reported include distal florets from the Miocene of Nebraska and the Pleistocene of North Carolina (Berry; Thomasson, 1987).

Setaria viridis subsp. *italica* is the most important member of the genus from an economic point of view. It is grown for hay, forage, and grain. It is a major cereal in China, and a minor cereal and bird-seed constituent in Eurasia (Arber, 1934, Clayton & Renvoize; De Wet *et al.*, 1979). Other species are also used for these purposes. The weedy *S. glauca* and *S. verticillata* are palatable to livestock (Melkania; Steel *et al.*). Members of the *S. sphacelata* complex are used as pasture grasses and harvested as cereals in African savannahs, and the shoots of *S. palmifolia* are cultivated for use as a vegetable in New Guinea. *Setaria palmifolia* is also harvested as a cereal in the Philippines and is cultivated as a greenhouse ornamental (Clayton & Renvoize; Rao *et al.*, 1987). An undetermined species of *Setaria* was used as a grain

in Tehuacán, Mexico, by 5500 B.C., and in Tamaulipas, Mexico, by 4000 B.C. (prior to the cultivation of *Zea Mays* L.). At least at the latter site, there is evidence of selection for grain size and processing techniques (Callen).

Many species of *Setaria* (*S. acromelaena* (Hochst.) Dur. & Schinz, *S. geniculata*, *S. glauca*, *S. homonyma* (Steudel) Chiov., *S. pallidifusca*, *S. palmifolia*, *S. Poiretiana* (Schultes) Kunth, *S. sphacelata*, *S. verticillata*, *S. viridis*) are noxious weeds in various parts of the world (Clayton & Renvoize; Hanson & Mason; Holm *et al.*; Jauzein; Steel *et al.*). *Setaria palmifolia* and *S. verticillata* are also hosts for maize dwarf mosaic virus and sugarcane mosaic virus (Rosenkranz).

REFERENCES:

- Under references for tribe see ARBER (1931, 1934); BHANWRA; BLAKE; BOLKHOVSKIKH *et al.*; BROWN (1977); BROWN *et al.* (1959); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); DAVIDSE & POHL (1974); DUNCAN; FERNANDES & QUEIRÓS; GIBBS RUSSELL (1983); GOULD (1975, 1979); GUTIERREZ *et al.*; HANSON & MASON; HATTERSLEY (1984); HALL; HOLM *et al.*; JONES & COILE; KANETA & SUGIYAMA; LELONG (1988); MACROBERTS; MCNEILL & DORE; OHWI; PLATZER; POHL (1980); PRENDERGAST & HATTERSLEY; RADFORD *et al.*; RENVOIZE; ROSENKRANZ; SCHUSTER; E. SMITH; SPRAGUE *et al.*; TATEOKA (1956a, b); THOMASSON (1987); TSVELEV (1976); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.
- AUQUIER, P. Les concepts de Dumortier dans le genre *Setaria* Beauv. (Poaceae). Bull. Jard. Bot. Natl. Belg. **49**: 427-433. 1979. [Typification and synonymy of Dumortier's taxa.]
- . Le genre *Setaria* Beauv. (Poaceae) en Belgique et au Grand-Duché de Luxembourg. Lejeunia II. **97**. 13 pp. 1979. [Good list of synonymy.]
- BEAL, W. J. Some monstrosities in spikelets of *Eragrostis* and *Setaria*. Bull. Torrey Bot. Club **27**: 85, 86. 1900.
- BELAEVA, V. A., & V. SIPLIVINSKY. In: Chromosome number reports. LXXIII. Taxon **30**: 829-861. 1981. [*S. viridis*, $2n = 18$.]
- BERRY, E. W. Additions to the Pleistocene flora of the Southern States. Torreyia **14**: 159-162. 1914. [Caryopsis from North Carolina attributed to *Chaetochloa* (= *Setaria*) sp.]
- BJÖRKQVIST, I., R. VON BOTHMER, Ö. NILSSON, & B. NORDENSTAM. Chromosome numbers in Iberian angiosperms. Bot. Not. **122**: 271-283. 1969. [Spanish *S. glauca*, $2n = 72$.]
- BOR, N. L. The species of *Setaria* P. Beauv. (sect. *Ptychophyllum* (A. Braun) Pilger) in India. Kew Bull. **1954**: 548-554. 1954.
- BUTZIN, F. Evolution der Infloreszenzen in der Borstenhirsen-Verwandschaft. Willdenowia **8**: 67-79. 1977. [A reduction series evident in *Setaria*, from 0-few bristles subtending each spikelet, to most branches being reduced to bristles and many bristles subtending each spikelet.]
- CALLAN, E. O. The first New World cereal. Am. Antiquity **32**: 535-538. 1967. [*Setaria* sp.]
- CHASE, A. The Linnaean concept of pearl millet. Am. Jour. Bot. **8**: 41-49. 1921. [*Panicum glaucum* is based on a species of *Pennisetum*, contrary to current thought; cf. TERRELL and others cited under *S. glaucum* above.]
- CHIKARA, J., & P. K. GUPTA. Numerical taxonomy in the genus *Setaria* (L.) Beauv. Proc. Indian Acad. Sci. Pl. Sci. **89**: 401-406. 1980. [Two subgenera (*Setaria* and *Ptychophyllum*) represented in data set; poor resolution of groups

- in cluster analysis, except for the OTUs of *S. sphacelata* (Schum.) Stapf & C. E. Hubb.]
- CLAYTON, W. D. Studies in the Gramineae: IX. Kew Bull. 20: 257-273. 1966. [Revision of the *S. sphacelata* complex in West Africa.]
- . Notes on *Setaria* (Gramineae). Kew Bull. 33: 501-509. 1979. [Three species complexes: *S. pumila* (= *S. glauca*), *S. sphacelata*, *S. palmifolia*.]
- DE WET, J. M. J., L. L. OESTRY-STIDD, & J. I. CUBERO. Origins and evolution of foxtail millets (*Setaria italica*). Jour. Agr. Trad. Bot. Appl. 26: 53-64. 1979. [Foxtail millet is likely a derivative of *S. viridis* but has probably been brought into cultivation independently in several places throughout the range of *S. viridis*; hybrids between them are fully fertile.]
- EMERY, W. H. P. A cyto-taxonomic study of *Setaria macrostachya* (Gramineae) and its relatives in the southwestern United States and Mexico. Bull. Torrey Bot. Club 84: 94-105. 1957a.
- . A study of reproduction in *Setaria macrostachya* and its relatives in the southwestern United States and northern Mexico. *Ibid.* 106-121. 1957b.
- FAIRBROTHERS, D. E. Morphological variation of *Setaria Faberii* and *S. viridis*. Brittonia 11: 44-48. 1959.
- FERNALD, M. L. *Setaria Faberii* in eastern America. Rhodora 46: 57, 58. 1944. [Key to *S. Faberi*, *S. viridis*, and *S. magna*.]
- GLUCHOFF-FIASSON, K., M. JAY, & M. R. VIRICEL. Flavone O- and C-glycosides from *Setaria italica*. Phytochemistry 28: 2471-2475. 1989.
- HACKER, J. B. Cytological investigations in the *Setaria sphacelata* complex. Austral. Jour. Agr. Res. 17: 297-301. 1966.
- . Polyploid structure in the *Setaria sphacelata* complex. Austral. Jour. Bot. 16: 539-544. 1968a.
- . Cytology of species hybrids in the *Setaria sphacelata* complex. *Ibid.* 551-554. 1968b.
- HERRMANN, W. Ueber das phylogenetische Alter des mechanischen Gewebesystems bei *Setaria*. Beitr. Biol. Pflanzen 10: 1-69. 1910. [Groups based on stem and leaf anatomy; *S. Faberi* and other species described.]
- HITCHCOCK, A. S. The North American species of *Chaetochloa*. Contr. U.S. Natl. Herb. 22: 155-208. 1920. [= *Setaria*; 60 spp.; good early monograph.]
- HSIA, C. A. Interspecific crosses in *Setaria*. III. Chromosomal variation in *S. italica-faberii*. Bot. Bull. Acad. Sinica 3: 1-11. 1949.
- HUBBARD, F. T. A taxonomic study of *Setaria italica* and its immediate allies. Am. Jour. Bot. 2: 169-198. 1915.
- JAUZEIN, P. Remarques sur le genre *Setaria* P. Beauv. en France. Monde Pl. 431: 9-12. 1988.
- KAWANO, S., & S. MIYAKE. The productive and reproductive biology of flowering plants. X. Reproductive energy allocation and propagule output of five congeners of the genus *Setaria* (Gramineae). Oecologia 57: 6-13. 1983.
- KEYS, C. E. Observations on the seed and germination of *Setaria italica* (L.) Beauv. Trans. Kansas Acad. Sci. 52: 474-477. 1949. [Germination flap of distal lemma described.]
- KIHARA, H., & E. KISHIMOTO. Bastarde zwischen *Setaria italica* und *S. viridis*. Bot. Mag. Tokyo 56: 62-67. 1942. [Hybrid fertile and looks like a large version of *S. viridis*; chromosomes form nine bivalents in the F₁.]
- KISHIMOTO, E. Chromosomenzahlen in den Gattungen *Panicum* und *Setaria*. I. Chromosomenzahlen einiger *Setaria*-Arten. Cytologia 9: 23-27. 1938. [Chromosome counts for six taxa.]
- KLIPHUIS, E. In: IOPB chromosome number reports. LVI. Taxon 26: 257-274. 1977. [*S. glauca*, 2n = 36; *S. viridis*, 2n = 18.]
- KOCH, H. Ueber die Involucra bei *Cynosurus* und *Setaria*. Bot. Zeit. 1: 249-253, 265-271, 281-286. 1843. [Numbers of bristles subtending spikelets in various parts of the panicle in *S. italica*, *S. viridis*, *S. verticillata*.]

- LAMSON-Scribner, F., & E. D. MERRILL. The North American species of *Chaetochloa*. U.S. Dept. Agr. Div. Agrost. Bull. No. 21. 44 pp. 1900. [= *Setaria*.]
- LI, H. W., C. H. LI, & W. K. PAO. Cytological and genetical studies of the interspecific cross of the cultivated foxtail millet, *Setaria italica* (L.) Beauv., and the green foxtail millet, *S. viridis* L. Jour. Am. Soc. Agron. **37**: 32-54. 1945. [*S. viridis* probable immediate progenitor of *S. italica*.]
- , C. J. MENG, & C. H. LI. Genetic studies with foxtail millet, *Setaria italica* (L.) Beauv. *Ibid.* **32**: 426-438. 1940. [Seed-coat color determined by three loci; endosperm characters determined by two loci; earhead types determined by two loci.]
- , & T. N. LIU. Problems in the breeding of millet (*Setaria italica* (L.) Beauv.). *Ibid.* **27**: 963-970. 1935.
- , W. K. PAO, & H. W. LI. Interspecific crosses in *Setaria*. II. Cytological studies of interspecific hybrids involving: 1, *S. Faberii* and *S. italica*, and 2, a three way cross, F₂ of *S. italica* × *S. viridis* and *S. Faberii*. Jour. Hered. **33**: 351-355. 1942.
- MELKANIAN, N. P. Studies on germination of *Setaria glauca* Beauv. New Botanist **15**: 29-32. 1988. [Germination inhibitor in seed coat.]
- MONACHINO, J. The type of *Setaria Faberii*. Rhodora **61**: 220-223. 1959.
- MORINAGA, T., E. FUKUSHIMA, T. KANÔ, Y. MARUYAMA, & T. YAMASAKI. Chromosome numbers of cultivated plants. II. Bot. Mag. Tokyo **43**: 589-594. 1929. [*S. italica* (= *S. viridis* subsp. *italica*), 2n = 18.]
- NARAYANASWAMI, S. Structure and development of the caryopsis in some Indian millets. VI. *Setaria italica*. Bot. Gaz. **118**: 112-122. 1956.
- NIKLAS, K. J. Pollen capture and wind-induced movement of compact and diffuse grass panicles: implications for pollination efficiency. Am. Jour. Bot. **74**: 74-89. 1987.
- NISHIMURA, M. Comparative morphology and development of *Poa pratensis*, *Phleum pratense* and *Setaria italica*. Jap. Jour. Bot. **1**: 55-85. 1922. [Depth and spread of roots greatest in *S. italica*.]
- PENSIERO, J. F. Notulae ad floram paraquaiensem, 8. *Setaria paraguayensis*, sp. nov. Candollea **41**: 469-472. 1986. [In subg. *Setaria*; scanning electron micrographs of distal lemma and barbs on bristles.]
- PITTY, A., D. W. STANFORTH, & L. H. TIFFANY. Fungi associated with caryopses of *Setaria* species from field-harvested seeds and from soil under two tillage systems. Weed Sci. **35**: 319-323. 1987. [Seeds of *S. viridis* and *S. Faberii* examined; degree of fungal colonization proportional to caryopsis size.]
- PODLECH, D., & A. DIETERLE. Chromosomenstudien an afghanischen Pflanzen. Candollea **24**: 185-243. 1969. [Afghan material of *S. viridis*, 2n = 18.]
- POHL, R. W. The genus *Setaria* in Iowa. Iowa State Coll. Jour. Sci. **25**: 501-508. 1951. [Six species, all illustrated and mapped.]
- . Notes on *Setaria viridis* and *S. Faberii* (Gramineae). Brittonia **14**: 210-213. 1962. [Chromosome counts, morphological differentiation.]
- RAMAKRISHNAN, P. S. Contributions to the ecological life-history of *Setaria glauca* Beauv. Jour. Indian Bot. Soc. **42**: 118-129. 1963. [Two ecotypes.]
- RAO, K. E. P., J. M. J. DE WET, D. E. BRINK, & M. H. MENGESHA. Intraspecific variation and systematics of cultivated *Setaria italica*, foxtail millet (Poaceae). Econ. Bot. **41**: 108-116. 1987. [Three cultivated races in *S. italica* (moharia, maxima, indica); *S. viridis* closest wild relative; hybrids fertile.]
- RAYNAL, D. J., & F. A. BAZZAZ. The contrasting life-cycle strategies of three summer annuals found in abandoned fields in Illinois. Jour. Ecol. **63**: 587-596. 1975. [*S. Faberii* compared with *Ambrosia artemisiifolia* L. and *Polygonum pennsylvanicum* L.]
- REEDER, J. R. *Setaria lutescens* an untenable name. Rhodora **53**: 27-30. 1951.
- ROMINGER, J. M. Taxonomy of *Setaria* (Gramineae) in North America. Illinois Biol. Monogr. **29**. viii + 132 pp. 1962. [Forty-three spp. in three subgenera]

(*Ptychophyllum*, *Paurochaetium*, *Setaria*); best available monograph for North and Central American species.]

- ROST, T. L. The ultrastructure and physiology of protein bodies and lipids from hydrated dormant and nondormant embryos of *Setaria lutescens* (Gramineae). *Am. Jour. Bot.* **59**: 607-616. 1972. [= *S. glauca*.]
- . The anatomy of the caryopsis coat in mature caryopses of the yellow foxtail grass (*Setaria lutescens*). *Bot. Gaz.* **134**: 32-39. 1973. [= *S. glauca*.]
- SACCHET, A. M. DE O. F., & I. I. BOLDRINI. In: Chromosome number reports. LXIX. *Taxon* **29**: 703-730. 1980. [Counts for 10 species of *Setaria*.]
- SCHLECHTENDAL, D. F. L. VON. Ueber *Setaria* P. B. *Linnaea* **31**: 387-509. 1861. [Worldwide monograph; taxa discussed under the genera in which they were described; thus, no new combinations made.]
- SCHOLZ, H. Kurze Mitteilung über bemerkenswerte intraindividuelle Variabilität von Mikrohaaren in der Gattung *Setaria* (Gramineae). *Willdenowia* **7**: 415-418. 1974.
- SCHONER, C. A., R. F. NORRIS, & W. CHILCOTE. Yellow foxtail (*Setaria lutescens*) biotype studies: growth and morphological characteristics. *Weed Sci.* **26**: 632-636. 1978.
- SCHREIBER, M. M., & L. R. OLIVER. Two new varieties of *Setaria viridis*. *Weed Sci.* **19**: 424-427. 1971. [Incl. key to common foxtails of temperate United States.]
- SOHNS, E. R. *Setaria*: fascicle organization in four species. *Jour. Wash. Acad. Sci.* **44**: 116-122. 1954.
- STAPP, O. *Setaria* or *Chaetochloa*? *Bull. Misc. Inf. Kew* **1920**: 124-127. 1920. [Discussion of usage, priority, typification.]
- . *Setaria glauca* and *S. lutescens*. *Ibid.* **1928**: 147-149. 1928. [Discussion of Linnaeus's concept of *S. glauca*.]
- STEEL, M. G., P. B. CAVERS, & S. M. LEE. The biology of Canadian weeds. 59. *Setaria glauca* (L.) Beauv. and *S. verticillata* (L.) Beauv. *Canad. Jour. Pl. Sci.* **63**: 711-725. 1983. [Detailed review of many aspects of life history of both species.]
- TERRELL, E. E. The correct names for pearl millet and yellow foxtail. *Taxon* **25**: 297-304. 1976. [Cf. A. CHASE, 1921.]
- VÁCHOVÁ, M., & V. FERÁKOVÁ. In: IOPB chromosome number reports. LXI. *Taxon* **27**: 375-392. 1978. [*S. verticillata*, $2n = 36$.]
- & ———. In: Chromosome number reports. LXIX. *Taxon* **29**: 703-730. 1980. [*S. verticillata*, $2n = 36$.]
- WILLIAMS, R. D., & M. M. SCHREIBER. Numerical and chemotaxonomy of the green foxtail complex. *Weed Sci.* **24**: 331-335. 1976. [Phenogram indicates close morphological relationship among various forms of *S. viridis*; *S. Faberii* closest to *S. viridis*, followed by *S. verticillata*; *S. glauca* least similar to green foxtail.]
- WOOD, C. E., JR. *Setaria Faberii* in North Carolina. *Rhodora* **48**: 391, 392. 1946.

20. *Paspalidium* Stapf, *Fl. Trop. Afr.* **9**: 582. 1920.

Stoloniferous, decumbent, or caespitose [rhizomatous], perennials [annuals]. Stem internodes hollow; nodes glabrous. Leaves with sheaths glabrous; ligule a fringe of hairs [fringed membrane]; blades linear [lanceolate], flat, folded or involute, glabrous to minutely pubescent, with truncate to rounded base, once-folded in bud; photosynthesis C_4 , biochemical pathway NADP-me. Inflorescences panicle, of 6-20 secund spike-like primary branches; rachides triquetrous, sometimes winged, ending in a bristle. Spikelets dorsiventrally compressed to

terete, disarticulating below the glumes, abaxial, secund, pedicellate (pedicel apices discoid), often subtended by bristles, solitary [paired], biseriate; proximal florets staminate [sterile], paleate [epaleate]. Calli undifferentiated. Glumes 2, unequal, glabrous, awnless; proximal glumes 1–5 nerved, encircling spikelet base; distal glumes equalling proximal lemmas, 5–7 [11] nerved. Proximal lemmas equalling and less firm than distal lemmas, glabrous, grooved, awnless, 5 nerved; distal lemmas cartilaginous, rugose, glabrous, grooved, acute to acuminate or mucronate, 5 nerved, with involute margins and a conspicuous germination flap. Distal paleas indurate, awnless, 2 nerved. Lodicules 2. Ovaries with styles fused or free, stigmas red. Caryopses (grains) small, smooth; endosperm containing only simple starch grains. Base chromosome number 9. LECTOTYPE SPECIES: *Paspalidium geminatum* (Forsskål) Stapf (*Panicum geminatum* Forsskål); see Pilger, Nat. Pflanzenfam., ed. 2. 14c: 29. 1940. (Name the Greek diminutive of *Paspalum*, alluding to a similarity between these genera.) — PASPALIDIUM.

A genus mainly of the Old World tropics, consisting of about 30 species of marshes, swamps, ditches, and other wet habitats in our region; also found in dry habitats in the tropics. The major center of diversity is in Australia (Webster, 1987, 1988). One species, *Paspalidium geminatum* (Forsskål) Stapf, Egyptian paspalidium, $n = 9, 18$, is naturalized in the area from Oklahoma, Texas, and Louisiana to South Carolina and Florida (Gould, 1975; Hall; MacRoberts; Radford *et al.*). It has imbricate spikelets arranged tightly on second racemose inflorescence branches. Gould (1971) treated a segregate of this species as var. *paludivagum* (Hitchc. & Chase) Gould, but its morphology overlaps to a large extent with that of the typical variety. Recent authors do not recognize the variety as distinct (Clewell, Hall, Wunderlin).

Paspalidium is considered closely related to *Setaria* and *Urochloa* (Blake; Pohl, 1980; Webster, 1988). It has the rugose distal lemma of those genera. The bristles terminating the branches and subtending some of the spikelets highlight its relationship to *Setaria*. Webster (1987, 1988) noted that the types of arrangements of spikelets and bristles in species of *Paspalidium* are encompassed by variation found in *Setaria*. The major character differentiating these genera is the arrangement of branches in the inflorescence, with *Paspalidium* having secund primary branches, and *Setaria* having quaquaversal branching (the branches originate on all sides of the main inflorescence axis) (Blake; Webster, 1988). The biochemical pathway in *Paspalidium* and *Setaria* is also the same (NADP-me), but differs from that in other genera with rugose distal lemmas, e.g., *Urochloa*, *Eriochloa* (PEP-ck). The phenetic analysis of Watson & Dallwitz indicates close relationships among *Paspalidium*, *Setaria*, and *Brachiaria* (= *Urochloa*, for the most part), with *Echinochloa* and *Paspalum* being more distant relatives (in a phenetic sense). Butzin (1970) placed *Paspalidium* in subtribe Paspalinae, with a hodgepodge of genera, including *Urochloa*,

Paspalum, *Echinochloa*, *Stenotaphrum*, *Alloteropsis*, and *Digitaria*, but excluding *Setaria*.

The chromosome base number of *Paspalidium* is nine, and the majority of counts are in line with this observation (Bolkhovskikh *et al.*). *Paspalidium flavidum* (Retz.) A. Camus, from India, contains diploid and hexaploid races (Gupta, 1969; Larsen; Malik & Tripathi; Mitra & Datta; Raman *et al.*, 1959b; Saxena & Gupta; Shanthamma *et al.*). However, it also has been reported to contain an aneuploid race with a base number of 11 ($n = 22$; Sharma & Sharma).

Nothing appears to be known about breeding systems in *Paspalidium*. It would serve as a good candidate for evolutionary studies, particularly with regard to its relationships with *Setaria*.

The exine of the pollen of *Paspalidium flavidum* is psilate. This condition differs from that in most other grasses, in which the pollen surface is faintly reticulate (Sidhu & Ahluwalia). However, more species and more genera must be examined before the significance of this character can be assessed.

In aquatic or semi-aquatic genera (including several species of *Paspalidium*), fruits may be dispersed on the feet of aquatic birds (Davidse, 1987). This speculation may seem reasonable, but evidence is needed to substantiate it.

Paspalidium flavidum and *P. geminatum* are listed as major or common weeds in many Old World tropical countries, and *P. obtusifolium* (Del.) Simpson is a weed of unspecified status in Morocco (Holm *et al.*).

REFERENCES:

- Under references for tribe see BAQUAR & SAEED; BHANWRA; BLAKE; BOLKHOV-SKIKH *et al.*; BROWN (1977); BURTON (1942); BUTZIN (1970); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1958, 1971, 1975, 1979); HALL; HOLM *et al.*; HUGHES; MACROBERTS; MALIK & TRIPATHI; MITRA & DATTA; OHWI; PARODI; POHL (1980); PRENDERGAST & HATTERSLEY; RADFORD *et al.*; RAMAN *et al.* (1959b); SAXENA & GUPTA; SHANTHAMMA *et al.*; SIDHU & AHLUWALIA; STAPF (1919-1934); TATEOKA (1965b); WEBSTER (1987, 1988); and WUNDERLIN.
- SHARMA, M. L., & K. SHARMA. In: IOPB chromosome number reports. LXI. Taxon 27: 375-392. 1978 [*P. flavidum*, $n = 22$.]

21. *Stenotaphrum* Trinius, Fund. Agrost. 175. 1822.

Stoloniferous [rhizomatous] perennials. Stems 10-60 cm high, branched; internodes solid to spongy; nodes glabrous. Leaves with sheaths keeled, margins glabrous to pubescent; ligule a fringed membrane; blades linear to lanceolate, obtuse at apex, folded or flat, glabrous, disarticulating from sheaths or not, with attenuate to truncate bases, folded in bud; photosynthesis C_4 , biochemical pathway NADP-me. Inflorescences paniculate, consisting of racemose, spike-like branches (sometimes greatly reduced) embedded in main axis, terminating in naked points; rachides hollow, disarticulating as units or at joints.

Spikelets lanceolate or ovate, dorsiventrally compressed, disarticulating along with main axis or its segments, abaxial, secund, sessile or short-pedicellate (pedicel apices truncate), solitary or paired, biseriate; proximal florets staminate or sterile, paleate [epaleate]. Calli undifferentiated. Glumes 2, unequal, awnless; proximal glumes nerveless [5–7 nerved]; distal glumes equalling proximal lemmas, [3] 5–9 nerved. Proximal lemmas equalling or slightly exceeding distal lemmas, chartaceous to coriaceous, acute to acuminate, awnless, [3] 7–9 nerved; distal lemmas cartilaginous, smooth or muricate, yellow, dull, glabrous, acute, awnless, 3–5 nerved, with involute (sometimes flat) margins and a conspicuous germination flap. Distal paleas indurate, awnless, 2 nerved. Lodicules 2. Ovaries with styles fused, stigmas white or red. Caryopses (grains) small, not grooved, smooth. Base chromosome number 9. TYPE SPECIES: *Stenotaphrum glabrum* Trin. = *S. dimidiatum* (L.) Brongn., the only species included in the genus at the time of its original description. (Name from Greek, *stenos*, narrow, and *taphros*, trench, in reference to the embedded branches in the main axis of the inflorescence.) — ST. AUGUSTINE GRASS.

A genus of seven species of tropical seacoasts, moist grasslands, river banks, disturbed areas, and lawns. Five species are restricted to tropical islands and coasts in the Indian and Pacific Oceans (Sauer).

Sauer considers *Stenotaphrum* to be most closely related to *Paspalidium*, and he suggested that *S. Helferi* Munro ex Hooker f., of forested streambanks in Southeast Asia, is the most primitive species in the genus and the least divergent from *Paspalidium*. Both genera have a chromosome base number of nine and utilize the same acid decarboxylation pathway (NADP-me). Webster (1987, 1988) disagreed and concluded instead that the spikelet characters and inflorescence modifications of *Stenotaphrum* pointed to a closer relationship with the monotypic genera *Thuarea* Pers. and *Uranthoecium* Stapf, of the Australasian region. Watson & Dallwitz concluded that *Pennisetum* (and its segregate *Beckeropsis*; subtribe Cenchrinae), *Paspalidium*, and *Digitaria* (subtribe Digitariinae) are most similar phenetically. However, overall similarity fails to give clear insights into phylogenetic relationships. Butzin (1970) placed *Stenotaphrum* in subtribe Paspalinae, which is included for the most part in subtribe Setariinae in the present treatment.

One species, *Stenotaphrum secundatum* (Walter) Kuntze, St. Augustine grass, $2n = 18, 27, 36$, (main axis of inflorescence corky, entire on back, racemes with 1–3 spikelets) has been widely introduced on the Atlantic and Gulf Coastal Plain of the Southeast, mainly for lawns and turfs. It may be a native of the Atlantic Coast of the United States from Florida to North Carolina, but this is uncertain (Sauer; Webster, 1988). It occurs along coasts on both sides of the Atlantic Ocean (Africa, Europe, South America, Central America, the West Indies, North America). It also occurs sporadically in the Pacific region, where it may also have been introduced (Sauer). Another species, *S.*

dimidiatum (L.) Brongn., native to the coasts of East Africa, Madagascar, southern India, Ceylon, and other islands in the Indian Ocean. $n = 18$, $28(?)$, $2n = 36$, 48 , (main axis of inflorescence membranaceous, sharply lobed on the back, racemes with 3–8 spikelets) has been reported from our region (Busey *et al.*), but its status is uncertain.

Stenotaphrum secundatum contains several distinctive variants. Diploids have yellow stigmas, sexual reproduction, normal meiosis (nine bivalents form), and high pollen fertility. Triploids have purple stigmas and are sterile. (Such plants are generally used for lawns.) Tetraploids also have purple stigmas and are sterile, but meiosis proceeds normally, except for the presence of quadrivalents (Long & Bashaw). Busey *et al.* conducted a most extensive morphometric analysis of the genotypes of *S. secundatum* that have been used agronomically in the United States. Twenty-six morphological and agronomic characters were measured for 94 genotypes, and the data matrix was analyzed using cluster analysis. The resulting clusters correlated strongly with the agronomic classification of cultivars, and more than 85 percent of the classified genotypes could be identified with a key that these authors generated. Their analysis also revealed that one of the genotypes was *S. dimidiatum*, a species previously unreported from the Southeast. Sauer discussed the characteristics of variants within *S. secundatum*, which he referred to as demes. He doubted whether the variants were actually true-breeding populations, however.

The segments of the swollen inflorescence axis bearing racemes may serve as propagules adapted to dispersal on sea currents. The segments remain buoyant for only about one week (Bor, 1960; Clayton & Renvoize; Davidse, 1987).

Stenotaphrum secundatum is an important lawn and turf grass in tropical and subtropical regions of the world, including the southeastern United States. It has also been used for soil erosion control (Webster, 1988). However, the sod in which it is transplanted can serve as a source for various weeds, especially if the grass should die (Shinners, 1962). *Stenotaphrum secundatum* is susceptible to cold and also to various diseases, such as rust (*Puccinia stenotaphri* (Syd.) Cummins; Todd, 1957) and brown patch (*Rhizoctonia solani* Kuehn; Zummo & Plakidas). It may also serve as a host for sugarcane mosaic virus (Todd, 1964).

REFERENCES:

Under references for tribe see ARBER (1934); BLOMQUIST; BOLKHOVSKIKH *et al.*; BOR (1960); BROWN (1950, 1951, 1977); BROWN *et al.* (1959); BUTZIN (1970); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; DAVIDSE (1987); GOULD (1975, 1979); JONES & COILE; MACROBERTS; PARODI; POHL (1980); POHL & DAVIDSE (1971); RADFORD *et al.*; TATEOKA (1965a); WATSON & DALLWITZ; WEBSTER (1987, 1988); and WUNDERLIN.

BUSEY, P., T. K. BROSCAT, & B. J. CENTER. Classification of St. Augustine grass. Crop Sci. Madison 22: 469–473. 1982. [Cluster analysis of cultivated genotypes; key to cultivars; *S. dimidiatum* new to North America.]

- LONG, J. A., & E. C. BASHAW. Microsporogenesis and chromosome numbers in St. Augustine grass. *Crop Sci.* Madison 1: 41-43. 1961. [Three cytological types and six morphological types characterized.]
- SAUER, J. D. Revision of *Stenotaphrum* (Gramineae: Paniceae) with attention to its historical geography. *Brittonia* 24: 202-222. 1972. [Most useful monograph available.]
- SHINNERS, L. H. Weed transport in St. Augustine grass sod in Texas. *Sida* 1: 98, 99. 1962. [Freezing kills *S. secundatum*.]
- SUZUKI, E., J.-I. OHNISHI, M. KASHIWAGI, & R. KANAI. Comparison of photosynthetic and photorespiratory enzyme activities between green leaves and colorless parts of variegated leaves of a C₄ plant, *Stenotaphrum secundatum* (Walt.) Kuntze. *Pl. Cell Physiol.* 27: 1117-1125. 1986. [All chloroplast enzymes with greatly reduced activities in colorless portions of leaves; cytoplasmic enzymes exhibited comparable activity levels in green and colorless regions.]
- TODD, E. H. Rust of St. Augustine grass in Florida. *Pl. Disease Rep.* 41: 650. 1957.
- . Sugarcane mosaic on St. Augustine grass in Florida. *Ibid.* 48: 442. 1964.
- ZUMMO, N., & A. G. PLAKIDAS. Brown patch of St. Augustine grass. *Pl. Disease Rep.* 42: 1141-1147. 1958. [Disease caused by *Rhizoctonia solani* Kuehn.]

Subtribe MELINIDINAE (Hitchc.) Pilger, *Nat. Pflanzenfam.*,
ed. 2. 14e: 95. 1940.

22. *Melinis* Palisot de Beauvois, *Essai Agrost.* 54. 1812.

Decumbent or stoloniferous [rhizomatous] perennials [annuals]. Stems 30-120 cm high, branched; internodes solid or spongy, viscid; nodes pubescent. Leaves with sheaths glabrous to pubescent or viscid-pubescent; ligules a fringed membrane or a fringe of hairs; blades linear, flat or involute, glabrous to glandular-pubescent, with cuneate to rounded bases, rolled in bud; photosynthesis C₄, biochemical pathway PEP-ck. Inflorescences paniculate, open [contracted], with capillary branches terminating in spikelets. Spikelets terete or laterally compressed, disarticulating below the glumes, pedicellate (pedicel apices discoid), solitary; proximal florets sterile [staminate], paleate or epaleate. Calli undifferentiated, sometimes hairy. Glumes 2, unequal, glabrous or pubescent, awned or awnless; proximal glumes minute, membranaceous, 0-1 nerved; distal glumes equalling proximal lemmas, membranaceous to chartaceous, [5] 7 nerved. Proximal lemmas chartaceous, awned from between apical lobes [awnless], [3] 5 nerved; distal lemmas membranaceous to cartilaginous, smooth, glabrous, obtuse to acute, bilobed, awnless, [1-] 5 nerved, with flat margins and an inconspicuous germination flap. Distal paleas apically notched, 2 nerved. Lodicules 2. Ovaries with styles free. Endosperm containing only simple starch grains. Chromosome base number 9. (Including *Rhynchelytrum* Nees, *Mildbraediochloa* Butzin.) TYPE SPECIES: *Melinis minutiflora* Beauv., the only species included in the genus at the time of its original description. (Name from Greek, *meli*, honey, and *-inis*, resembling, in reference to the honey-like odor produced by glands of these plants.)

A genus of 22 species of open woodlands, grasslands, scrublands, and disturbed open areas in equatorial and southern Africa, and widely introduced and adventive in the other tropical parts of the world (Zizka). Roshevits and Clayton & Renvoize suggested that *Melinis minutiflora*, molasses grass, $2n = 36, 40$, is also native to Brazil, but this is unlikely (Jacques-Félix; Zizka). Two species occur in our area as naturalized weeds. *Melinis minutiflora* may be distinguished from its close relative, *Melinis repens* (Willd.) Zizka (*Rhynchelytrum repens* (Willd.) C. E. Hubb., *Tricholaena rosea* Nees, *Rhynchelytrum roseum* (Nees) Stapf & C. E. Hubb. ex Bews), Natal grass, $n = 9, 18, 2n = 36$, by the straight-backed (rather than gibbous) glumes, glandular foliage, and smaller (2 mm vs. 5 mm, excluding the awns and indument), purplish (not white or pink), glabrous or short-pubescent (rather than densely long-pilose) spikelets. *Melinis minutiflora* was introduced into Florida as an experimental forage grass and now occurs infrequently as a weed. *Melinis repens* has become a common weed of open disturbed areas in the warmer parts of the Americas (Gould, 1979) and has also become established along the Gulf Coast from Florida to Texas, and westward to Arizona. Its colorful inflorescences and habit of growing in large, dense colonies make it a striking grass.

Melinis and *Tricholaena* Schrader ex Schultes comprise subtribe Melinidinae (Hitchc.) Pilger (Butzin, 1971; Clayton & Renvoize; Zizka). These genera differ from other Paniceae in their laterally compressed spikelets, reduced proximal glumes, often emarginate or bilobed and awned distal glumes, cartilaginous distal lemmas, and expansive panicles. They have the PEP-carboxykinase decarboxylation system, which is uncommon elsewhere in the Paniceae (see *Eriochloa*). Subtribe Melinidinae has sometimes been accorded tribal rank and has been circumscribed in various ways. Roshevits included four other genera (*Arthropogon* Nees, *Achlaena* Griseb., *Thysanolaena* Nees, and *Triscenia* Griseb.) that belong to other subtribes or even subfamilies (e.g., *Thysanolaena* in the Arundinoideae), according to most modern treatments. Bentham included even more disparate elements in this group, which he considered close to tribe Andropogoneae Dumort. He included *Rhynchelytrum* (but not *Melinis*) in *Panicum* as a section.

Melinis minutiflora has been cultivated for forage, especially in South America, and is considered to be one of the best fodder crops in the tropics (Roshevits). However, it is probably more important as a weed. In certain parts of Hawaii it has become the dominant ground cover and is excluding native vegetation (pers. obs.). It is also listed as a weed in several South and Central American countries, as well as in Australia, India, and South Africa (Holm *et al.*).

REFERENCES:

Under references for tribe see BENTHAM; BOLKHOVSKIKH *et al.*; W. V. BROWN & EMERY (1958); CHIPPINDALL; CLAYTON & RENVOIZE; CLEWELL; GOULD (1975, 1979); HITCHCOCK & CHASE (1951); HOLM *et al.*; JONES & COILE; NASH (1912); POHL (1980); PRENDERGAST & HATTERSLEY; ROSENKRANZ; ROSHEVITS; WEBSTER (1987, 1988); and WUNDERLIN.

- BUTZIN, F. Der Umfang der Melinideae (Gramineae, Panicoideae) und die neue Gattung *Mildbraediochloa*. *Willdenowia* 6: 285-289. 1971.
- FOSBERG, F. R. Polynesian plant studies. 6. *Tricholaena* Schrader (Poaceae) in the Pacific Islands. *Smithson. Contr. Bot.* 47: 1-3. 1981. [*Rhynchelytrum* merged with *Tricholaena*; earliest Pacific collections of *T. repens* (Willd.) Hitchc. (= *M. repens*) are from Hawaii in 1909.]
- JACQUES-FÉLIX, H. Le *Melinis minutiflora* est une Graminée africaine. *Bull. Mus. Natl. Hist. Nat. Paris. IV. (Adansonia)* 9: 461, 462. 1987.
- REEDER, J. R. The embryo in grass systematics. *Am. Jour. Bot.* 44: 756-768. 1957. [Illustrations of embryos of *Panicum clandestinum* L., *Rhynchelytrum roseum* (Nees) Stapf & C. E. Hubb. ex Bews (= *Melinis repens* (Willd.) Zizka), *Cenchrus pauciflorus* Benth., *Antheophora hermaphrodita* (L.) Kuntze.]
- ZIZKA, G. Revision der Melinideae Hitchcock (Poaceae, Panicoideae). *Bibliot. Bot.* 138: 1-149. 1988. [Recognizes *Tricholaena* Schrader ex Schultes and *Melinis* Beauv., but merges *Rhynchelytrum* Nees with *Melinis*.]

THE GENERA OF PEDALIACEAE IN THE SOUTHEASTERN UNITED STATES¹

STEPHEN D. MANNING²

PEDALIACEAE R. Brown, Prodr. 519. 1810, "Pedalinae," nom. cons.
(PEDALIUM, SESAMUM, OR BENE FAMILY)

Annual or perennial herbs [sometimes with short, swollen stems and tuberous roots], [or small trees with swollen stems, or shrubs with or without swollen main branches], of disturbed areas such as dry fields and roadsides, sometimes near coasts. Stems erect [to prostrate], usually unbranched [or branched], unarmed [or less often spiny], usually

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project currently made possible through the support of the National Science Foundation Grant BSR-8716834 (N. G. Miller, principal investigator), under which this account was prepared, and BSR-8717333 (C. E. Wood, Jr., principal investigator). The 138th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39**: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. The references that I have not verified are marked with asterisks.

I gratefully acknowledge all of the assistance I have received in the preparation of this paper. Norton G. Miller, Carroll E. Wood, Jr., and Gordon C. Tucker all took time out from otherwise busy schedules to provide information, perspectives on the taxonomic literature, and/or comments on successive drafts of the manuscript. Norton Miller and Carroll Wood reviewed the manuscript editorially. The staffs of the following libraries gave prompt assistance in finding literature that was sometimes difficult to obtain: The New York State Library, especially Alta Beach, Senior Librarian; the libraries of the Gray Herbarium and Arnold Arboretum, Harvard University; and the library of the Missouri Botanical Garden. The curators of the following herbaria sent specimens or provided hospitality and access to the collections under their care during my visits: BH, CU, FLAS, GH, MO, NCU, NY, NYS, US, and USF. I also thank the curators of other herbaria in the Southeast and elsewhere who provided information and/or searched for specimens at my request. This paper is published as Contribution Number 689 of the New York State Science Service.

²Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230.

© President and Fellows of Harvard College, 1991.

Journal of the Arnold Arboretum, Supplementary Series **1**: 313-347. 1991.

pubescent and with usually stalked, 4-celled, grayish-white mucilage secreting glands. Leaves opposite, subopposite, or sometimes alternate [or subwhorled], exstipulate; blades simple or occasionally trifoliolate [or palmately compound]; if simple, entire to deeply 3 [or more] lobed, shape ovate, cordate, elliptical, obovate, [suborbicular, or lorate], sometimes varied within plants; if trifoliolate, leaflets obovate, elliptical, or ovate; margins sometimes crenate or irregularly lobed; apices acute to obtuse or rarely truncate [or emarginate]; bases acute, obtuse, cordate, cuneate, or rarely truncate; main lateral veins ca. 3-10; blades thinly to densely pubescent, with indumentum similar to that on stems, including mucilage secreting glands above and usually more densely below [rarely glabrous]; petioles also pubescent and with mucilage glands. Inflorescences axillary; flowers solitary or occasionally in few-flowered cymes, usually subhorizontally oriented [or suberect]; pedicels with indumentum similar to that of the stem, flowers sometimes subtended by 1 or 2 sometimes deciduous, rudimentary or \pm subulate, linear, [or rarely subhemispherical] bract(s), reduced petiolate leaves, or rudimentary flower(s). Flowers perfect, perianth 5-merous. Calyx synsepalous, green, lobes usually at least slightly unequal, entire, narrowly triangular, narrowly ovate, [more broadly ovate or triangular], or rarely linear persistent or deciduous in fruit, with indumentum similar to leaves. Corolla sympetalous, pink, purple, white, [blue, or yellow], sometimes with darker lines [or other patterns], zygomorphic, bilabiate or nearly so [or the lobes subequal], the lower lobe(s) usually the longest, tube often curved at base [sometimes funnel shaped or cylindrical, often slightly gibbous adaxially, or rarely spurred at base], lobes valvate or nearly so, entire [rarely fringed]; sparsely to densely pubescent and glandular. Stamens 4, didynamous, alternate with corolla lobes, included in the corolla tube [or the longer two exserted]; adaxial staminode present or absent; filaments inserted on corolla tube near its base; anthers oblong to sagittate, dorsifixed [or pendent from apex of connective], thecae subparallel [or divergent], longitudinally dehiscent; pollen grains solitary [or in tetrads in *Sesamothamnus*], [5] 7-13 colpate, oblate, suboblate, prolate, or spheroidal. Gynoecium superior, syncarpous, carpels [1] 2-4, locules [1] 2-4, [if more than 1] separated by a septum [or septa], each locule [sometimes] divided into 2 compartments nearly from base to apex by a secondary partition; ovules [1-] numerous, anatropous, subhorizontal [to erect or pendent], [solitary or] in a longitudinal row in [1, 2, or] each of the compartments, placentation axile [basal in *Linariopsis*]; disk hypogynous, subannular [or asymmetrical]; style filiform, longer than staminal filaments; stigma usually bilobed. Fruits [spiny, ridged, winged, or barbed] subobconoidal to ellipsoidal or subcylindrical, [subovoid, subglobose, obovoid, or subdiscoidal and horizontally flattened] loculicidal capsules, with [or without] an apical beak or 2 or apparently 4 apical horns [or other appendages], dehiscent at least near apex along the secondary partitions [or indehiscent], suberect [to horizontal] in axils. Seeds slightly to strongly flattened [or nearly round in transverse section], unwinged [or with 1-3 wings], obovate, [oblong,

elliptical, or suborbicular] in outline, glabrous, light brown to black [or white], outer seed coat surface smooth, rugose, or verrucose [or with other patterns]; endosperm thin and oily; embryo sac of Polygonum type; embryo development of Onagrad type. Base chromosome number 8, possibly 13. TYPE GENUS: *Pedaliium* D. Royen ex L.

A relatively small Old World family of 13 genera and about 60 species, sometimes but not here united with the Martyniaceae (about 3 genera, 13 species) or Trapellaceae (1 genus, 2 species). Within the Pedaliaceae the genera are distinct, but species within a genus are usually less clearly defined. The family is most diverse in Africa (one genus, *Uncarina* (Baillon) Stapf, is endemic to the Malagasy Republic) and is represented in India, Sri Lanka (*Pedaliium*, *Sesamum* L.), and Australia (*Josephinia* Vent.). The New World representatives of the family are introduced.

Ceratotheca triloba (Bernh.) Hooker f. and *Sesamum orientale* L., sesame, have spread from cultivation and are of sporadic occurrence in the southeastern United States. Although the number of independent introductions of *C. triloba* is unknown, introductions of sesame have been frequent. It is not known how long naturalized populations of either species persist, but some populations appear to be self seeding.

The family is characterized by the four-celled mucilage glands that occur on most organs. Abortive flowers subtending fully developed ones, fruit morphology, and pollen characters also distinguish most Pedaliaceae from members of related families. These distinguishing features are discussed in turn below.

The mucilage glands of Pedaliaceae consist of four- to occasionally eight-celled capitula (the cells of which are delimited by thick vertical walls) borne on short uniseriate and usually unicellular stalks. The caputular cells have walls arching outward from the stalk. The mucilage is the product of the breakdown of cellulose in these thick walls; the cell lumina are almost full of mucilage (Solereider). The plants become slimy when wet, at least partly as a result of the heads breaking off the stalks, thereby releasing mucilage. The function of the mucilage glands is not certain, although sesame plants with many glands have been shown to wilt less than others with few glands during a period of drought and also to be more resistant to high soil-water content during a period of excess rainfall (Langham, 1945a, see under *Sesamum*; includes photographs of mucilage glands). Mucilage glands of this type are unknown elsewhere in the plant kingdom (Ihlenfeldt, 1967b), although nonmucilage producing capitate or subcapitate trichomes with different configurations of cells occur in Trapellaceae, Martyniaceae, Gesneriaceae, Acanthaceae, and Bignoniaceae. The trichomes of Martyniaceae produce sticky secretions (Thieret, Thorne).

The basic inflorescence type in the Pedaliaceae is a simple dichasium. Typically, however, dichasia are reduced to single flowers that are sometimes accompanied by one or two rudimentary lateral flowers. These may be secretory or excretory and thus have been termed extrafloral

nectaries. In some species all three flowers of the dichasium develop fully (rarely up to eight flowers have been reported in aberrant individuals of *Sesamum orientale*). Field observations reveal that insects visit the flowers but not the extrafloral nectaries, even though they contain small quantities of sugars (Monod). These abortive flowers develop to varying degrees. Their morphology and anatomy are thoroughly addressed by Monod, and their development is traced by Singh (1960b). Extrafloral nectaries in related families are often of types not homologous to those just described.

The nature of the fruits also serves both to distinguish Pedaliaceae from related families and to distinguish genera within the family. Mature fruits are nonfleshy. Those of some genera (e.g., *Ceratotheca* Endl. and *Sesamum*) are dehiscent, while those of others (e.g., *Dicerocaryum* Bojer and *Josephinia*) are indehiscent. Partial indehiscence is noted in some individuals of each of our species. Within this overall framework, great variation in fruit wall ornamentation has evolved in the family, e.g., terminal beaks (*Sesamum*), angular horns (*Ceratotheca*), monstrous barbs (*Harpagophytum* (Burch.) DC. ex Meisn., *Uncarina*), and wings (*Holubia* Oliver, *Pterodiscus* Hooker). Though the fruits of our genera are different enough to distinguish them easily, they are more similar to each other than are those of most other genera in the family. Pedaliaceous fruits have been placed in three groups according to the planes of symmetry of their ornamentation (Ihlenfeldt, 1965, 1976b): without emergences (*Sesamum* and *Sesamothamnus* Welw.); with emergences in the vertical plane perpendicular to the septum (*Ceratotheca* horns, *Dicerocaryum* spines); and with emergences in other vertical planes (other genera), whether these emergences are wings, spines, or barbs. The other vertical planes form a relatively large angle with the plane of the septum, as in the wings of *Pterodiscus* and barbs of *Harpagophytum*. In some genera the emergences sometimes also occur in planes at a relatively small angle with the plane of the septum, e.g., the spines of *Rogeria* Gay ex Delile and *Josephinia*. In *Linariopsis* Welw., the fruits do not fall neatly into the above classification because emergences occur in planes both perpendicular to the septum and elsewhere.

The secondary partitions of fruits also serve to distinguish Pedaliaceae from related families. Although not universally present, such partitions often are, as in fruits of species in both of our genera. These traverse the middle of each ovary locule, and in our representatives of the family the fruits dehisce loculicidally along them. When secondary partitions are absent in Pedaliaceae, this character state appears to be derived (Ihlenfeldt, 1965). Comparable fruits with locule partitions are not found in the related Bignoniaceae, Martyniaceae, Trapellaceae, or Scrophulariaceae.

Pollen grains in the family are five or more colpate, with the colpi typically not reaching the polar regions. Similar grains occur in many Bignoniaceae (as only one of several distinct types found there), but bignoniaceous pollen is typically tricolpate (Ihlenfeldt, 1967b). Pollen

very similar to that of Pedaliaceae occurs in some Acanthaceae (Bremekamp), e.g., *Thomandersia* Baillon. Pollen of Martyniaceae (Ihlenfeldt, 1967b; Thieret; Alvarado; Bretting & Nilsson), Scrophulariaceae (Cronquist, 1981) and Trapellaceae (Ihlenfeldt, 1967b) differs from that of the Pedaliaceae, as discussed below. Though the Pedaliaceae are relatively stenopalynous, differences among genera can be distinguished, mainly the exine of the mesocolpi, which varies from thinner to thicker at the edges of colpi than in between. *Sesamum* and *Ceratotheca* are among the genera in which the mesocolpi contain a more or less amorphous layer between the nexine and sexine. Such a layer has not been detected in all genera of the family. Pollen differences (Straka; Straka & Ihlenfeldt) correspond approximately to the three tribes of the Pedaliaceae *sensu* Ihlenfeldt (1967b).

Early classifications of Pedaliaceae (e.g., Bureau) emphasized the distinctiveness of gynoeceal and fruit characters and the closeness to Bignoniaceae and Martyniaceae in other respects, while differing in the ranks assigned to suprageneric taxa. The comprehensive treatment of the family by Bentham (Bentham & Hooker) established four tribes, one of which included genera now segregated as the Martyniaceae. The other tribes of Pedaliaceae *sensu* Bentham & Hooker were Pedalieae Meisn. (anther locules separate and subpendulous from the filament apex, ovaries two locular, the locules lacking secondary partitions (*Pedalium*, *Pterodiscus*, *Harpagophytum*)); Sesameae (Endl.) Meisn. (anther locules parallel or diverging at the base, ovaries two locular, the locules with a secondary partition, some locules with many seeds (*Rogeria*, *Sesamothamnus*, *Sesamum*, *Ceratotheca*)); and Pretreeae Bentham (anther locules parallel or diverging at the base, ovaries from one to four locular, the locules often with a secondary partition, and one or two seeds per locule (*Pretrea* = *Dicerocaryum*, *Linariopsis*, *Josephinia*)). Until revised by Ihlenfeldt (1967b), this classification has been followed by most workers, except for the removal of Martyniaceae as a separate family, as discussed below.

Recent work in the family by Ihlenfeldt and his associates has led to the current classification of Pedaliaceae, set forth most completely, along with a thorough review of earlier taxonomic treatments, by Ihlenfeldt (1967b). Subfamilies are not recognized, and Martyniaceae and Trapellaceae are excluded. Emphasizing stamen morphology, Ihlenfeldt divided the family into three tribes of somewhat different circumscription from Bentham: Sesamothamneae Ihl. (shrubs with stems succulent at the base, anthers dorsifixed, thecae parallel, pollen in tetrads (*Sesamothamnus*)); Sesameae (herbs or subshrubs, anthers dorsifixed, thecae parallel, pollen solitary (*Sesamum*, *Ceratotheca*, *Dicerocaryum*, *Linariopsis*, *Josephinia*)); and Pedalieae (subshrubs or annual or perennial herbs, anther thecae diverging toward the base and pendent from the tips of the filaments, pollen solitary (*Pedalium*, *Holabium*, *Harpagophytum*, *Pterodiscus*, *Uncarina*, *Rogeria*)). The most significant modification is the isolation of *Sesamothamnus*.

Oliver considered the bilocular ovary without secondary partitions to be primitive in the Pedaliaceae and unilocular ovaries or secondary partitions derived. Accordingly (in the context of Bentham's classification) he considered the Pedalieae basal in the family, despite their specialized fruits. He considered the Pretreeae (partitions originating from the septum of the fruit) derived from this group and the Sesameae (secondary partitions from the adaxial and abaxial walls of the fruit) derived from the Pedalieae through *Harpagophytum*, which is characterized by adaxial and abaxial ingrowths that do not however reach all the way to the placenta. He considered *Pedaliium* the closest relative of *Trapella* Oliver (Trapellaceae), noting geographic proximity and similarities in seed arrangement and structure. Thus, Oliver based his phylogeny largely on a single character set, ovary structure. While his phylogenetic hypothesis has not been accepted by later workers in the family, his analysis should be taken seriously to the degree that ovary structure may be conservative and thus entitled to greater weight than other characters, such as the external ornamentation of fruits, which are seen to have potential coevolutionary significance.

Ihlenfeldt placed the three tribes in a phylogenetic sequence in which Pedalieae are separated first and the other tribes are separated very soon thereafter. Within the Sesameae, *Sesamum* is considered most primitive, with subsequent divergences involving *Josephinia*, *Linariopsis*, *Ceratotheca*, and *Dicerocaryum*. Support for the primitiveness and isolated position of *Sesamothamnus* is drawn from the shrubby habit, broadly winged seeds (like some in the Bignoniaceae), pollen in tetrads (like some Bignoniaceae), hawkmoth-pollinated-type flowers (corolla spurred, lobes subequal), leaves borne from spines that are alternately arranged along the stem, and racemelike inflorescences. Its closeness to *Sesamum* and *Ceratotheca* is inferred from the similarity of the anthers and fruits, although fruits of *Sesamothamnus* are laterally compressed.

Members of the Pedaliaceae commonly are found in warm, relatively dry habitats with well-drained soils, although these may be near sea-coasts or other water bodies. They are typically able to survive periods of water shortage. Adaptations such as swollen stems (*Sesamothamnus*, *Pterodiscus*), tuberous roots (*Harpagophytum*, *Pterodiscus*), or subsucculent leaves (*Holubia*, *Pterodiscus*, *Pedaliium*, *Harpagophytum*) may serve as water holding organs in some genera. Most are annuals. The monotypic *Holubia* is a facultative biennial, and in other genera (e.g., *Dicerocaryum*, *Ceratotheca*, and *Sesamum*) some species (including both of ours) can be either annuals or perennials. Sites with a high water table are unfavorable, as has been documented for sesame.

Flowers of southern African genera of the family have been classified by Vogel as melittophilous (*Dicerocaryum*, *Sesamum*, *Ceratotheca*) or sphingophilous (*Holubia*, *Sesamothamnus*). Nevertheless, the flowers of *Sesamum orientale* are normally self-pollinated in cultivation, although bee pollination occurs also.

Much of the chemical research in the family has been on *Sesamum orientale* and *Harpagophytum procumbens* (Burch.) DC. ex Meisn. (Hegnauer). Iridoid monoterpenes (Seigler), flavones (Gibbs), iridoid glycosides, lignans, phenolic compounds, and miscellaneous storage carbohydrates have been identified in Pedaliaceae. Aluminum accumulators are unknown. Ellagic acid and alkaloids are also unknown, but the phenolic glycoside orobanchin, accumulated in members of the Orobanchaceae, also a member of the Scrophulariales, is present (Gibbs). The presence of mucilage is in contrast to almost all Martyniaceae, Bignoniaceae, Acanthaceae, and Scrophulariaceae (Gibbs). Seco-iridoids are absent, as they are throughout the Scrophulariales; the iridoids identified to date are all 10-hydroxylated carboxylic iridoids, as in Martyniaceae but unlike those of the Acanthaceae. These and other types of iridoids are present in Bignoniaceae and Scrophulariaceae (Dahlgren *et al.*). Calcium oxalate crystals, when present, are usually small and either solitary or clustered (Solereder).

Characteristics of the wood anatomy of Pedaliaceae include simple vessel perforation plates, vessel pits with sometimes wide apertures (perhaps a reflection of habitats promoting high transpiration), circular to oval lateral wall pits, simple pits in imperforate tracheary elements, septate fibers, multiseriate rays at least as abundant as uniseriate ones, relatively few procumbent cells in rays, and apotracheal banded parenchyma. In general, wood of Pedaliaceae resembles that of Martyniaceae (Carlquist).

Anther-wall formation in species that have been investigated is of the commonest "dicotyledonous" type, in which the inner secondary parietal layer develops directly into the tapetum with suppression of periclinal division, and the outer secondary parietal layer gives rise to two layers, the outer one forming the endothecium and the inner the "middle layer" (Davis). The tapetum is glandular, and its cells become multinucleate. In *Pedaliium Murex* L. these nuclei later fuse, resulting in polyploid nuclei (Davis).

Outgrowths on some pedaliaceous fruits are adaptations for animal seed dispersal (Cronquist, 1988), for example, the trample-burs of *Harpagophytum*, in which seeds are trampled out of the fruits and into the ground (Van der Pijl). In others the outgrowths are wings, and the fruits are wind dispersed. In our species of *Sesamum* and *Ceratotheca*, the terminal and sometimes complete basipetal dehiscence of the capsules allows local distribution of seeds. The seeds nearest the base appear least likely to come out quickly. In a minority of species of *Ceratotheca* and *Sesamum*, structural features of the fruits may exaggerate this tendency to retard dispersal of the basal seeds (Stopp; Ihlenfeldt, 1967a; Abels; Roth). These involve basal thickening of the fruit wall or the formation of swollen "seed pockets" near the bases of all or only two of the fruit compartments. These features, however, are not constant within species and may be pathological (Ihlenfeldt, 1967a); they apparently have not been reported in either of our species. No reports of endozoochorous dispersal of the seeds are known.

The Pedaliaceae are placed by Cronquist (1988) in the Scrophulariales, an order characterized by often bilabiate tubular corollas with fewer stamens than corolla lobes. All of the chemical and nonchemical characters surveyed by Dahlgren (1980) and Dahlgren *et al.* (1981) support this placement; all characters surveyed are shared with some or all other families in the order. The Pedaliaceae are placed by Thorne in the Bignoniales, an order nearly the same in its circumscription as the Scrophulariales *sensu* Cronquist. Differences in circumscription between Scrophulariales of Cronquist and Bignoniales of Thorne involve taxa relatively distant from the Pedaliaceae (Loganiaceae [Buddlejaceae], Oleaceae, Plantaginaceae).

Families most often cited as close relatives of Pedaliaceae include Trapellaceae and Martyniaceae (included in Pedaliaceae as a subfamily by Goldberg and without infrafamilial rank by Cronquist), Bignoniaceae (e.g., Bruce, 1953a), Scrophulariaceae (Baillon), and Acanthaceae (Bremekamp). The Pedaliaceae may be derived from the immediate ancestors of the Bignoniaceae (Takhtajan, Thorne). However, wood anatomy of the Pedaliaceae is not conclusively more similar to that of the Bignoniaceae than to that of any other members of the Scrophulariales (Carlquist). Ihlenfeldt (1967b) considered the Acanthaceae-Scrophulariaceae to be basal, and Bignoniaceae, Pedaliaceae, and Martyniaceae/Trapellaceae derived in that order. Relationships between Pedaliaceae and each of these families are outlined below.

The monotypic Trapellaceae are aquatic plants of Asia almost universally believed to be related to the Pedaliaceae, with authors differing, however, on the nature of the relationship. They are distinguished from Pedaliaceae in having only two fertile stamens and an inferior ovary. They were included by Oliver (as a monotypic tribe) and Cronquist (without formal infrafamilial rank) within the Pedaliaceae. Li considered them a family linking the Pedaliaceae and Myoporaceae. Ihlenfeldt (1967b) placed them slightly closer to Martyniaceae than Pedaliaceae. Takhtajan considered them to be derived but separate from the Pedaliaceae.

Pedaliaceae have been termed the Old World analogue of the New World Martyniaceae (Thieret). The Martyniaceae are a family usually distinguished from the Pedaliaceae in having parietal rather than axile placentation, although some authors doubt that the distinction between these two types of placentation is sufficient for a familial differentiation (Singh, 1960b; Cronquist, 1981). There are several other features that distinguish the two families. In the Pedaliaceae pollen is five or more colpate with vertical colpi usually not reaching the polar regions, inflorescences are axillary (although racemelike on short shoots in *Sesamothamnus*), fruits are hard when mature, and $x = 8$ or 13, in contrast to pollen apolar and without vertical colpi, terminal racemes, fleshy mature fruits, and $x = 15$ or 16 in the Martyniaceae (Bretting & Nilsson, Bentham & Hooker, Thieret, Raven). The wood anatomy of Martyniaceae is similar to that of herbaceous Pedaliaceae (Carlquist).

The Pedaliaceae "can be interpreted as an Old World branch of the Bignoniaceae Juss. with specialized (e.g., anemochorous and zoochorous) fruits" (Ihlenfeldt & Grabow-Seidensticker; see under *Sesamum*). There are several other features that distinguish typical Pedaliaceae from typical Bignoniaceae (Bruce, 1953a; Ihlenfeldt, 1967b; Raven). Members of the Pedaliaceae are typically herbaceous, have four-celled mucilage glands, two-carpellate ovaries with locules often divided into two compartments by secondary partitions, simple leaves, unilateral disks, obliquely campanulate corollas, thin endosperm, wingless seeds, and $x = 8$ or 13. Bignoniaceae are typically woody, have several types of glands but not of the pedaliaceous type, two-loculate ovaries rarely subdivided by secondary partitions, compound leaves, symmetrical disks, large and variable corollas, no endosperm, winged seeds, and $x = 20$. There are some exceptions, however. For example, in our representatives of Pedaliaceae the disk is subannular.

The Scrophulariaceae normally have capsules with loculicidal to septicidal or rarely irregular or poricidal dehiscence, usually tricolporate pollen, and base chromosome numbers as low as six. The Pedaliaceae have loculicidal capsules or indehiscent fruits, polycolpate pollen, and a base chromosome number of eight or thirteen (Cronquist, 1981; Raven).

The chief proponent of a close relationship between Pedaliaceae and Acanthaceae was Bremekamp, in part on the basis of similarity between pollen of *Thomandersia* and that of Pedaliaceae. Several characters distinguish the two families: Acanthaceae typically have cystoliths, seeds with a retinaculum (persistent hooked funiculus), transverse ridges between leaf petioles, and, like all other families, lack four-celled mucilage glands of the pedaliaceous type. Those representatives of Acanthaceae not sharing the above characters are transitional to Scrophulariaceae rather than Pedaliaceae (Cronquist, 1981). Bremekamp's suggestion that *Thomandersia* be placed in the Pedaliaceae, whether or not the two families are joined, has not been followed.

Some genera of the family other than our two are also of economic importance (Uphof). For example, *Pedaliium Murex* has been reported to have various traditional medicinal uses, and its leaves are edible. Fruits of *Harpagophytum* and other genera with hooked fruits become stuck on livestock (Metcalf & Chalk, Pijl) and the tubers of *H. procumbens* are medicinal (Uphof). Synergistic effects of extracts from *Sesamum orientale* and other members of the family have been reported to increase insecticidal effectiveness. Extracts of *Pedaliium Murex* have been reported to be effective mosquito larvicides (Kalyanasundaram & Das).

Because of the interest in improving sesame as a commercial crop, the research and literature on the family are dominated by studies on this species. These are summarized in the following treatment of *Sesamum*.

REFERENCES:

- ABELS, J. Die Gattungen *Ceratotheca* Endl. und *Dicerocaryum* Boj. (Monographien der afrikanischen Pedaliaceae III-IV). Mem. Soc. Broteriana 25: 1-358. 1975.

[The most thorough existing treatment of these two genera, including morphology, morphometrics, anatomy, development, geography, ecology, distribution, associated plants, taxonomic history and revision, evolutionary hypotheses, and an extensive bibliography.]

- ALVARADO, J. L. Catalogo palinológico para la flora de Veracruz. No. 15. Familia Pedaliaceae. *Biotica* 8: 381–385. 1983. [Incl. thorough description and photographs of *S. orientale* pollen by light and scanning electron microscopy.]
- BACKER, C. A. Pedaliaceae. In: C. G. G. J. VAN STEENIS, Fl. Malesiana I. 4: 216–219. 1951. [Pedaliaceae including Martyniaceae; *Sesamum*, *Josephinia*.]
- & R. C. BAKHUIZEN VAN DEN BRINK, JR. Fl. Java 2: 542–544. 1965. [*Sesamum*, *Josephinia*.]
- BAILEY, L. H. Manual of cultivated plants. Revised ed., completely restudied. 1116 pp. New York. 1949. [*Ceratotheca triloba*, *Sesamum orientale*, 908.]
- , E. Z. BAILEY, & L. H. BAILEY HORTORIUM STAFF. Hortus third. xiv + 1290 pp. New York & London. 1976. [*Ceratotheca*, 249; *Sesamum*, 1039.]
- BAILLON, H. Notes sur les Pédalinées. Bull. Mens. Soc. Linn. Paris 84: 665–671. 1887. [*Ceratotheca* treated as a section of *Sesamum*; gynoeceal characters emphasized, Martyniaceae thus separated.]
- BATSON, W. T. A guide to the genera of the plants of eastern North America, ed. 3, revised. iv + 203 pp. Columbia, South Carolina. 1984. [Incl. both our genera.]
- BEDIGIAN, D., D. S. SEIGLER, & J. R. HARLAN. Sesamin, sesamolin and the origin of sesame. Biochem. Syst. Ecol. 13: 133–139. 1985. [Wild *S. orientale* in India proposed as progenitor of cultivated sesame; lignans in *S. orientale*, some but not all other species of *Sesamum*, and some but not all other genera of Pedaliaceae; not in members of Bignoniaceae, Acanthaceae, and other families, although previously reported in some members of those families; potentially toxic biologically active substances in sesame oil; seed dormancy in wild *Sesamum* species.]
- BENTHAM, G., & J. D. HOOKER. Gen. Pl. 2(2): viii + 533–1279. London. 1876, reprinted 1965. [Pedaliaceae R. Br., *sensu lato*, 1054–1060, divided into four tribes, including one for Martyniaceae; treatment by BENTHAM.]
- BERNHARDI, J. J. Ueber die Gattungen der Sesameae. Linnaea 16: 29–42. 1842. [Incl. original description of *Ceratotheca triloba*, but as part of a new genus *Sporledera* (= *Ceratotheca* in part); other species of *Ceratotheca* retained in *Ceratotheca*; *Sesamum* as presently understood divided into three genera.]
- BOLKHOVSKIKH, Z., V., GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. In: A. A. FEDEROV, ed., Chromosome numbers of flowering plants. (Russian and English prefaces.) 926 + 3 pp. Leningrad. 1969. [Pedaliaceae, 485, 486; *Ceratotheca*, *Pedaliium*, *Rogeria*, *Sesamum*.]
- BOULTER, D. The molecular evolution of higher plant cytochrome *c*. Pure Appl. Chem. 34: 539–552. 1973. [Phylogenetic trees based on cytochrome *c* sequences; includes *Sesamum orientale* and 20 species from other families.]
- BREMEKAMP, C. E. B. The position of the genus *Thomandersia* Baill. Rec. Trav. Bot. Néerl. 39: 166–175. 1942. [Suggests placement in Pedaliaceae or uniting Pedaliaceae and Acanthaceae.]
- BRETTON, P. K., & S. NILSSON. Pollen morphology of the Martyniaceae and its systematic implications. Syst. Bot. 13: 51–59. 1988. [Apparently no overlap with Pedaliaceae; separation of the two families supported.]
- BROWN, R. Pedaliaceae. In: Prodrum Florae Novae Hollandiae et Insulae Van-Diemen 1: 519–520. 1810. [Incl. *Josephinia*.]
- BRUCE, E. A. Notes on African Pedaliaceae. Kew Bull. 8: 417–429. 1953a. [Pre-1953 subdivisions of *Sesamum* criticized; classification of *Sesamothamnus*, *Josephinia* (disjunct between Africa and Australia), *Pterodiscus*, and *Dicercocaryum* also discussed.]
- . Pedaliaceae. In: W. B. TURRILL & E. MILNE-REDHEAD, eds., Fl. Trop. East Africa, Vol. 2. 24 pp. London. 1953b. [Seven genera.]

- BUREAU, E. Monographie des Bignoniacées. iv + 215 pp. Paris. 1864. ["Bignoniacées" an order, divided into fifteen groups, some now recognized as genera, some as tribes, and some as families; "Sésamées" (= *Sesamum* + *Ceratotheca*) and "Pédalinées" (other Pedaliaceae + Martyniaceae) considered distant from each other within this alliance because of differences in gynoeceal structure.]
- CANDOLLE, A. P. DE. Sesameae. Prodr. 9: 249–257. 1845. [Incl. Martyniaceae; 12 genera in two tribes, one of them (Eusesameae = Sesameae) with *Sesamum* (5 spp.), *Ceratotheca* (1 sp., not *C. triloba*), and *Sporledera* (2 spp. including *S. triloba*, now placed in *Ceratotheca*.)]
- CARLQUIST, S. Wood anatomy of Martyniaceae and Pedaliaceae. Aliso 11: 473–483. 1987. [Comparisons with other members of Scrophulariales, including Bignoniaceae.]
- & S. ZONA. Wood anatomy of Acanthaceae: A survey. Ibid. 12: 201–227. 1988. [Similar to that of Pedaliaceae and other Scrophulariales.]
- CLARKE, C. B. Pedaliaceae. In: J. D. HOOKER. Fl. British India 4: 386, 387. 1884. [*Sesamum*, *Pedaliaceae*.]
- CLEWELL, A. F. Guide to the vascular plants of the Florida panhandle. viii + 607 pp. + unpagged index. Tallahassee, Florida. 1985.
- COOK, C. D. K., B. J. GUT, E. M. RIX, J. SCHNELLER, & M. SEITZ. Water plants of the world. viii + 561 pp. The Hague. 1974. [Trapellaceae, incl. illustrations, 538, 539.]
- COOKE, T. Pedaliaceae. Fl. Presidency Bombay 2: 411–414. 1905, reprinted 1958. [*Ceratotheca triloba* and *Sesamum orientale* cultivated in India.]
- CORNER, E. J. H. The seeds of dicotyledons, Vol. 1. x + 311 pp. Cambridge and New York. 1976. [Pedaliaceae, 216; *Uncarina*, *Harpagophytum*, *Sesamum*, *Trapella* (Trapellaceae).]
- CRONQUIST, A. An integrated system of classification of flowering plants. xviii + 1262 pp. New York. 1981. [Pedaliaceae, 966–968; Scrophulariales bibliography, 940–944.]
- . The evolution and classification of flowering plants, ed. 2. x + 555 pp. 1 unpagged chart. Bronx, New York. 1988. [Scrophulariales, 431–436; Pedaliaceae, 434, 513, incl. Martyniaceae and Trapellaceae.]
- DAHLGREN, R. M. T. A revised system of classification of the angiosperms. Bot. Jour. Linn. Soc. 80: 91–124. 1980. [Chemical and non-chemical characters surveyed; Pedaliaceae belong in Scrophulariales.]
- , S. ROSENDAL-JENSEN, & B. J. NIELSEN. A revised classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149–204 in D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. x + 295 pp. New York. 1981. [Chemical characters surveyed; iridoids present in Pedaliaceae are similar to those of Martyniaceae, and like some of those of Bignoniaceae and Scrophulariaceae in being 10-hydroxylated carboxylic iridoids, but are unlike those of Acanthaceae.]
- DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Pedaliaceae, 10, 14, 205; incl. microsporogenesis.]
- DECAISNE, J. Revue du groupe des Pédalinées. Ann. Sci. Nat. Bot. V. 3: 321–336. 1865. [Excl. both *Sesamum* and *Ceratotheca*.]
- DIELS, L. A. Engler's Syllabus der Pflanzenfamilien, ed. 11. xliii + 419 pp. Berlin. 1936. [*Sesamum*, *Pretrea* (= *Dicerocaryum*), 351.]
- DUNCAN, W. H., & J. K. KARTESZ. Vascular flora of Georgia, an annotated checklist. xii + 143 pp. + index. Athens, Georgia. 1981. [*Sesamum orientale* in the Coastal Plain.]
- ELIAS, T. S. Extrafloral nectaries: Their structure and distribution. Pp. 174–203 in B. BENTLEY & T. S. ELIAS, eds., The biology of nectaries. x + 259 pp. New York. 1983. ["Occasional" stalked nectaries on pedicel in Pedaliaceae; five of 12 families in Scrophulariales have extrafloral nectaries.]

- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. xii + 539 pp. Waltham, Massachusetts. 1952. [Pedaliaceae (*Ceratotheca*, *Josephinia*, *Sesamothamnus*, *Sesamum*), 315, 316.]
- GAERTNER, J. Fructibus et seminibus plantarum. Vol. 1. clxxxii + 384 pp. 79 pls. Stuttgart. 1788. [*Pedaliium*, 276, 277, pl. 63.]
- GIBBS, R. D. Chemotaxonomy of flowering plants. Vol. 3. Pp. 1275-1980. Montreal. 1974. [Survey with scattered references to Pedaliaceae throughout, not all chemically based; chemical data, 1777, 1778, 1789-1791, 1794, 1795, compared with other families of Scrophulariales.]
- GOLDBERG, A. Classification, evolution, and phylogeny of the families of dicotyledons. Smithson. Contr. Bot. 58: 1-314. 1986. [Pedaliaceae, 296; incl. Martyniaceae as a subfamily.]
- GOOD, R. Features of evolution in the flowering plants. x + 405 pp. New York. 1956, reprinted 1974. [Pedaliaceae, 69; a family with a low species/genus ratio (ca. 4).]
- HEGNAUER, R. Chemotaxonomie der Pflanzen, Bd. 5. 506 pp. Basel und Stuttgart. 1969. [Pedaliaceae, 299-302; anatomical, morphological, and chemical characters summarized.]
- HEINE, H. Pedaliaceae. In: F. N. HEPPER, ed., Fl. West Trop. Africa, ed. 2. 2: 388-391. 1963. [*Sesamum*, *Ceratotheca*, *Pedaliium*, *Rogeria*.]
- HOOKE, J. D. *Ceratotheca triloba*. Bot. Mag. 114: Pl. 6974. [4 pp. text.] 1888. [Valid, effective publication of the combination (see ABELS); compared with *Sesamum*.]
- HUMBERT, H. Les Pédaliacées de Madagascar. Adansonia II. 2: 200-215. 1962. [*Uncarina*, *Pedaliium*, *Pretrea* (= *Dicerocaryum*), *Sesamum*.]
- . 179e Famille Pédaliacées. Pp. 5-46 in: Flore de Madagascar et des Comores. iv + 163 pp. Paris. 1971. [*Uncarina* endemic, other genera introduced.]
- HUTCHINSON, J. The families of flowering plants arranged according to a new system based on their probable phylogeny, ed. 3. xix + 968 pp. Oxford. 1973, reprinted 1979. [Pedaliaceae, 482, 483.]
- IHLENFELDT, H.-D. Über die systematische Gliederung der Pedaliaceae nach makroskopisch erkennbaren Merkmalen. Ber. Deutsch. Bot. Ges. 77: 27-31. 1965 [1964]. [Distinguishing features of Pedaliaceae, emphasizing fruits, which are classified into three groups based on their emergences.]
- . Bemerkungen zur Taxonomie der südwestafrikanischen Pedaliaceae. Mitt. Bot. München 6: 593-612. 1967a. [*Ceratotheca* and other genera.]
- . Über die Abgrenzung und die natürliche Gliederung der Pedaliaceae R. Br. Mitt. Staatsinst. Allg. Bot. Hamburg 12: 43-128. 1967b. [Family monograph, 12 genera in three tribes, one (*Sesameae*) including *Sesamum* and *Ceratotheca*.]
- . In: E. LAUNERT, ed., Fl. Zambesiaca 8(3). 118 pp. London. 1988. [Pedaliaceae, 80-114; eight genera; *Ceratotheca triloba* and other species illustrated; keys and descriptions.]
- & H. HARTMANN. Die Gattung *Harpagophytum* (Burch.) DC. ex Meisn. (Monographie der Afrikanischen Pedaliaceae II). Mitt. Staatsinst. Allg. Bot. Hamburg 13: 15-69. 1970.*
- & H. STRÄKA. Über die Morphologie und Entwicklungsgeschichte der Früchte von *Uncarina* (Baill.) Stapf (Pedaliaceae). Zeitschr. Bot. 50: 154-168. 1962.
- KALYANASUNDARAM, M., & P. K. DAS. Larvicidal & synergistic activity of plant extracts for mosquito control. Indian Jour. Med. Res. 82: 19-23. 1985. [*Pedaliium Murex*.]
- LE MAOUT, E., & J. DECAISNE. Traité général de botanique descriptive et analytique. x + 746 pp. Paris. 1868. [Sésamées (= Pedaliaceae), 198-200; two tribes, *Sesamum* in one, *Pedaliium*, *Harpagophytum*, *Josephinia*, *Pretrea* = *Dicerocaryum* and genera of Martyniaceae in the other; proposed relationships to Bignoniaceae and Gesneriaceae.]

- LI, H.-L. Trapellaceae, a familial segregate from the Asiatic flora. Jour. Wash. Acad. Sci. **44**: 11-13. 1954. [Segregated from Pedaliaceae.]
- LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. Ed. 2. Miami. 1976.
- LUBBOCK, J. A contribution to our knowledge of seedlings, Vol. 2. iv + 646 pp. London. 1892. ["Pedalineae," 345, 346; fruit and seed morphology of both Pedaliaceae and Martyniaceae; seedling characters for Martyniaceae only.]
- MACROBERTS, D. T. A documented checklist and atlas of the vascular flora of Louisiana. Dicotyledoneae, Fagaceae to Zygophyllaceae. Bull. Mus. Life Sci. Louisiana State Univ., Shreveport **9**. Pp. xxxvii-li + 537-756 + A1-A15 + unpagged bibliogr. Shreveport, Louisiana. 1989.
- MATTHEW, K. M., & N. RANI. Pedaliaceae. In: K. M. MATTHEW, Fl. Tamilnadu Carnatic **3**: 1137-1140. 1983. [*Sesamum*, *Pedaliium* in a part of India.]
- MEISNER, K. F. Plantarum vasculariarum genera secundum ordines naturales digesta eorumque differentiae et affinitates tabulis diagnosticis expositae. Vol. 1. Tabulae diagnosticae. iv + 442 pp. Lipsiae. 1840 [1836-1843]. [Tribes Pedalieae, Sesameae, 298.]; *Ibid.* Vol. 2. Commentarius. i + 402 pp. Lipsiae. 1840 [1836-1843]. [Tribes Pedalieae, Sesameae, 206.]
- MELCHIOR, H. A. Engler's Syllabus der Pflanzenfamilien, ed. 12. Vol. 2. vi + 666 pp. Berlin. 1964. [Pedaliaceae, 460, 461; four tribes, incl. Trapelleae (= Trapellaceae).]
- METCALFE, C. R., & L. CHALK. Anatomy of the dicotyledons. Vol. 2. x + pp. 725-1500. Oxford. 1950. [Pedaliaceae, 1012-1014.]
- MONOD, T. Nectaires extra-floraux et fleurs avortées chez les Pédaliacées (note préliminaire). Bull. Mus. Hist. Nat. Paris IV. (B. Adansonia) **8**: 103-115. 1986. [Careful study of abortive flowers provisionally termed extra-floral nectaries in several genera including *Sesamum* and *Ceratotheca*.]
- NETOLITZKY, F. Anatomie der Angiospermen-Samen. Handb. Pflanzenanat. II. vi + 365 pp. Berlin. 1926. [*Sesamum*, *Harpagophytum*, 284, 285, 291.]
- OLIVER, F. W. On the structure, development, and affinities of *Trapella* Oliv., a new genus of Pedalineae. Ann. Bot. **2**: 75-115. 1888.
- PAL, A., & N. PARIA. On the affinity of some economic Pedaliaceae with special reference to pollen morphology and a note on their occurrence in the Salt Lake City, Calcutta, West Bengal. Jour. Econ. Taxon. Bot. **8**: 191-195. 1986. [*Pedaliium*, *Sesamum*.]
- PIJL, L. VAN DER. Principles of dispersal in higher plants. ed. 3. x + 215 pp. Berlin, Heidelberg, and New York. 1982. [Trample burs discussed, 79, 80.]
- PURSEGLOVE, J. W. Tropical crops. Dicotyledons. Vol. 2. viii + pp. 333-719. New York. 1968. [Pedaliaceae, 430-435, incl. *Sesamum* spp., *Ceratotheca sesamoides*.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Guide to the vascular flora of the Carolinas. iv + 383 pp. Chapel Hill, North Carolina. 1964.
- RAO, V. S. The floral anatomy of some bicarpellatae III. Pedaliaceae. Jour. Univ. Bombay **23**: 18-26. 1955.*
- RAVEN, P. H. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. **62**: 724-764. 1975. [Base chromosome numbers in Pedaliaceae 8 and 13.]
- RHEENEN, H. A. VAN. Intergeneric hybridization between *Ceratotheca sesamoides* Endl. and *Sesamum indicum* L. Nigerian Jour. Sci. **4**: 251-254. 1971 [1970]. [Hybrid sterile.]
- ROTH, I. Fruits of angiosperms. Encyclopedia of plant anatomy. xvi + 675 pp. Berlin and Stuttgart. 1977. [Pedaliaceae, 8, 65, 587, 591, 599.]
- ROXBURGH, W. Flora indica or descriptions of Indian plants. Vol. 3. viii + 875 pp. Serampore. 1832. [*Sesamum* (sic), 100, 101; earliest known placement of *S. indicum* in synonymy under *S. orientale*; *Pedaliium*, 114, 115.]

- SAYEEDUD-DIN, M. Some common Indian herbs with notes on their anatomical characters. Jour. Bombay Nat. Hist. Soc. **41**: 113–115. 3 pls. 1939. [Anatomy and distribution of hairs, of which three types are distinguished in addition to mucilage hairs, and leaves, including stomata, in *Sesamum laciniatum*; comparison with other plants.]
- SCHNARF, K. Vergleichende Embryologie der Angiospermen. vii + 354 pp. Berlin. 1931. [Pedaliaceae, 185; *Sesamum* and *Ceratotheca* both have micropylar and chalazal endosperm haustoria.]
- SEIGLER, D. S. Terpenes and plant phylogeny. Pp. 117–148 in D. A. YOUNG & D. S. SEIGLER, eds., Phytochemistry and angiosperm phylogeny. x + 295 pp. New York. 1981. [Iridoid monoterpenes present in Pedaliaceae and all other families of Bignoniales (= Scrophulariales) but only rarely elsewhere.]
- SINGH, S. P. Morphological studies in some members of the family Pedaliaceae. Thesis. Agra, India. 1958.*
- . Morphological studies in some members of the family Pedaliaceae. Agra Univ. Jour. Res. Sci. **9**: 217–220. 1960a.*
- . Morphological studies in some members of the family Pedaliaceae—I. *Sesamum indicum* D.C. Phytomorphology **10**: 65–82. 1960b. [Morphology, anatomy, and organogeny of flowers and extrafloral nectaries (abortive flowers), microsporogenesis (anther endothecium undergoes fibrous wall thickenings before dehiscence as in most angiosperms, contrary to some earlier literature), megasporogenesis, endosperm, embryology, seed and fruit development; comparison with other genera; literature review.]
- SMALL, J. K. Flora of the southeastern United States, ed. 2. xii + 1394 pp. New York. 1913. [*Sesamum*, 1366; *Ceratotheca* not added by Small until 1933.]
- . Manual of the southeastern flora. xxii + 1554 pp. Published by the author, New York. 1933. [*Sesamum* and *Ceratotheca*, 1243.]
- SOLEREDER, H. Systematic anatomy of the dicotyledons. English transl., Vol. 1. xii + 644 pp. Oxford. 1908. [Pedaliaceae, 611, 612.]
- SRINIVASAN, A. R. Contribution to the morphology of *Pedaliium Murex* Linn. and *Sesamum indicum* D.C. Proc. Indian Acad. Sci. B. **16**: 155–164. 1942. [Microsporangium development, micro- and megasporogenesis, endosperm development, fertilization, embryology, chromosome numbers.]
- STAFF, O. Pedaliaceae. Engler & Prantl, Nat. Pflanzenfam. IV. **3**: 253–265. 1895. [Fourteen genera, includes *Trapella* but excludes Martyniaceae.]
- . Pedalineae. In: W. T. THISLTON-DYER, ed., Fl. Trop. Africa **4**(2): 538–570. 1906. [Incl. 12 genera, most still recognized, with keys to and descriptions of genera and species, including ours, and extensive bibliography; only *Trapella* and *Uncarina* of the 14 genera treated in the immediately preceding reference not present.]
- STOPP, K. Antitelechoe Einrichtungen bei den Gattungen *Sesamum*, *Rogeria* und *Psilocaulon*. Beitr. Biol. Pflanzen **37**: 63–76. 1962. [Fruit structures retarding seed dispersal in *Ceratotheca* and other genera.]
- STRAKA, H. Über die Bedeutung der Pollenmorphologie für die Systematik. Ber. Deutsch. Bot. Ges. **77**: 31–39. 1965 [1964]. [Pollen of Pedaliaceae divided into three categories, two further subdivided; this classification correlates highly with the most recent subdivision of the family (IHLENFELDT, 1967b).]
- & H.-D. IHLENFELDT. Pollenmorphologie und Systematik der Pedaliaceae R. Br. Beitr. Biol. Pflanzen **41**: 175–207. 1965. [Pollen described for 12 genera of Pedaliaceae; incl. *Sesamum*, *Ceratotheca*, Martyniaceae, and Trapellaceae.]
- TAKHTAJAN, A. Flowering plants origin and dispersal. x + 310 pp. English transl. with revisions and additions. Washington. 1969. [Pedaliaceae, 231.]
- THEOBALD, W. L., & D. A. GRUPE. In: M. D. DASSANAYAKE, ed., A Revised Handbook to the Flora of Ceylon **3**. vii + 499 pp. Washington & New Delhi. 1981. [Pedaliaceae, 321–327; *Pedaliium*, *Sesamum*.]

- THIERET, J. W. The Martyniaceae in the southeastern United States. Jour. Arnold Arb. 58: 25-39. 1977. [Pedaliaceae kept separate.]
- THORNE, R. F. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35-106. 1976. [Pedaliaceae, 91, 92; placed in Bignoniales (\cong Scrophulariales).]
- UPHOF, J. C. T. Dictionary of economic plants, ed. 2. viii + 591 pp. Lehre, Germany. 1968. [*Ceratotheca sesamoides*, food, 119; *Harpagophytum procumbens*, medicinal, 262; *Pedaliium Murex*, food and medicinal, 392; *Rogeria adenophylla*, medicinal and food, 453; *Sesamum alatum*, *S. angustifolium*, *S. orientale*, food and other uses and *S. calycinum*, food, 481.]
- VOGEL, S. Blütenbiologische Typen als Elemente der Sipplengliederung Dargestellt Anhand der Flora Südafrikas. Bot. Studien 1: 1-338. 5 pls. 1954. [Pedaliaceae, 257, 258; flowers of *Pretrea* (= *Dicerocaryum*), *Sesamum*, *Harpagophytum*, *Pterodiscus*, and *Ceratotheca* probably bee pollinated, those of *Holubia* and *Sesamothamnus* probably hawkmoth pollinated.]
- WELWITSCH, F. Ordo Bignoniaceae. Trans. Linn. Soc. London 27: 49-55. 1869. ["Subordo Sesameae," 49-52; "Subordo Pedalineae", 53-55, incl. original description of *Linariopsis*.]
- WUNDERLIN, R. P. Guide to the vascular plants of central Florida. xi + 472 pp. Tampa, St. Petersburg, Fort Myers, and Sarasota, Florida. 1982. [*Ceratotheca triloba*, *Sesamum orientale*, 336.]

KEY TO THE GENERA OF PEDALIACEAE IN THE
SOUTHEASTERN UNITED STATES

General characteristics: Erect annual or perennial herbs with stalked, capitate 4-celled mucilage secreting glands and uniseriate glandular and nonglandular hairs on nearly all parts; leaves opposite, subopposite, or rarely alternate, exstipulate; inflorescences axillary, flowers usually solitary, but often with abortive flowers also at the pedicel bases (showing the flowers to be terminal members of reduced dichasia); perianth pentamerous; calyx synsepalous, lobes slightly unequal; corolla sympetalous, subbilabiate, usually subhorizontal, curved at the base; fertile stamens 4, inserted in corolla tube near base, included, didynamous or nearly so, anthers dorsifixed, thecae subparallel; gynoecium syncarpous, superior, each locule divided into 2 compartments nearly from base to apex by a secondary partition; style 1, included; stigma 1, bilamellate when open; ovules numerous, attached along the axis in a longitudinal row in each of the compartments; fruits suberect, subcylindrical loculicidal capsules, when mature usually more or less tetrangular with longitudinal grooves at the septum and secondary partitions, the whole or the distal portion dehiscing basipetally along secondary partitions; seeds obovate in outline, glabrous, unwinged.

- A. Fruit not or hardly subtruncate at apex, without angular horns but with a conspicuous terminal beak; flowers with a staminode; leaves ovate, oblong, or rarely obovate; lower leaves often 7 or more cm long or wide, sometimes deeply 3 lobed or occasionally trifoliate, if less than 7 cm long, not broadly subcordate or shallowly 3 lobed1. *Sesamum*.
- A. Fruit subtruncate at apex, with a subdeltoid to linear horn at each of the outer edges of the apex, terminal beak inconspicuous or absent; flowers without a staminode; leaves broadly ovate-subcordate to less often rotund, elliptical, or slightly obovate; lower leaves not exceeding 7 cm in length or width, sometimes broadly subcordate or only shallowly 3 lobed.....2. *Ceratotheca*.

1. *Sesamum* Linnaeus, Sp. Pl. 2: 634. 1753; Gen. Pl. ed. 5. 282. 1754.

Annual or perennial herbs, often in dry, disturbed areas and along roadsides. Stems erect [to prostrate], usually unbranched [or branched], terete near bottom, becoming \pm tetragonal. Leaves usually drying light green [or darker], slightly [to strongly] discolorous [or concolorous], opposite, subopposite, or rarely alternate; blades simple or occasionally trifoliate [or palmately compound]; if simple, unlobed to deeply 3 [or more] lobed, shape ovate, elliptical, obovate, [suborbicular, or lorate], often varied within plants, if trifoliate, leaflet shape ovate, elliptical, or ovate, sometimes asymmetrical; apices usually acute [or obtuse]; bases acute, obtuse, or rarely truncate, main lateral veins ca. [3-] 6-10; margins sometimes irregularly lobed or crenate; blades usually sparsely to densely pubescent [rarely glabrous]. Flowers solitary or rarely in simple few-flowered cymes; flowers usually subtended by 1 or 2 rudimentary or \pm subulate, linear [or subhemispherical] bract(s), and sometimes by 1 or 2 rudimentary flower(s) in the axil(s) of the bract(s). Calyx lobes slightly unequal, narrowly triangular, valvate, usually persistent [or deciduous] in fruit. Corolla pink, white, purple, or blue, sometimes with dots or other patterns of contrasting hues including red, black, or yellow, subbilabiate, usually subhorizontal, the lower lip as long as or longer than the upper; lobes entire or nearly so. Staminode 1; pollen 7-13 colpate, oblate to prolate or spheroidal. Carpels 2 (4), locules 2 (4). Fruits elliptical to weakly obovate [or ovate] in outline, with apical beaks. Seeds slightly [to strongly] flattened [or nearly round in transverse section], with 2 inconspicuous fringes [or 1 or 2 prominent fringes] around the seed, unwinged [or with 3 wings, 1 apical and 2 basal-lateral, borne from seed fringe locations], surfaces smooth, light brown (to black or white), [foveolate, or otherwise patterned]; endosperm cellular; embryo straight. Chromosome number $n = 13$, [16, or 32], base number (probably) 8. (Including *Simsimum* Bernh., *Gangila* Bernh., *Sesamopteris* DC., and *Volkameria* L. ex Kuntze.) LECTOTYPE SPECIES: *S. orientale* L.; see Seegeler. (Name of uncertain but ancient origin, apparently ultimately based on Near Eastern names for sesame (Bedigian & Harlan, 1986).) — SESAME, BENNE, BENNISEED; see Bedigian & Harlan (1986), Brown (1957), and Morton for extensive lists of other vernacular names in the Old World, the Philippines, and the New World, respectively; see Nicolson *et al.* for interpretation of vernacular names in Van Rhee's *Hortus Malabaricus*.

A genus of 21 species in four sections (Ihlenfeldt & Grabow-Seidensticker), largely restricted to tropical and subtropical Africa, but with some species in Asia. *Sesamum orientale*, sesame, has become naturalized in scattered locations from plants under cultivation, including coastal and other places from at least South Carolina to Texas (the

largest number of herbarium specimens from Florida).³

The correct name for sesame has been a matter of uncertainty since its description by Linnaeus as two separate species, *Sesamum orientale* (entire, ovate-oblong leaves) and *S. indicum* L. (lower leaves three lobed). De Candolle (1829) treated only *S. indicum*, provided a list of pre-Linnaean and nonbinomial synonyms, and suggested that *S. orientale* should probably be combined with *S. indicum*. However, he did not unite the two species, as emphasized by Seegeler (see Nicolson *et al.* for a contrary conclusion). The two species were united by Roxburgh (1832), followed by Graham (1839), under the name *S. orientale*. The union of these species by De Candolle (1845) under the name *S. indicum* does not have priority, and the correct name is *S. orientale* unless an earlier combination under the name *S. indicum* is found. Nevertheless, although some later authors (e.g., Gandhi, Van Steenis, and Matthew & Rani) have used *S. orientale*, others have adopted *S. indicum*.

Much morphological variation occurs in *Sesamum orientale*, including the "wild gingelly of Malabar" (John *et al.*) and many cultivars. Although the variation is often geographically correlated, no subspecies or varieties are recognized formally. Factor, discriminant, and cluster analyses have been used to evaluate this intraspecific variation; although most of this variation appears continuous, those plants with tetracarpellate capsules formed a statistically discernible group, as did some geographically defined groups of plants to a lesser extent (Bedigian, Smyth, & Harlan).

Worldwide, *Sesamum orientale* now consists mostly of plants in or derived ultimately from cultivation. Cultivation is most extensive in Asia, especially in India and China. Large acreages also occur in Sudan, Mexico, and Myanmar (Burma). Sudan, however, has accounted for over half of world exports because less than 10 percent of the total acreage probably enters world trade (Weiss). Africa accounts for about 70 percent of world exports of sesame. In Mexico and Venezuela cultivation as a cash crop is also significant, unlike in the United States. Some attempts have been made to cultivate sesame nearly everywhere it will grow, including the southeastern United States, where historically significant efforts to cultivate it have been centered in South Carolina

³Extended observations are needed to assess the extent of persistence of individual populations of sesame outside of cultivation. Although it has not been included in several floristic treatments within our area (e.g., Clewell, Long & Lakela, MacRoberts, and Radford *et al.*), it has in others (e.g., Batson, Small (1913, 1933), Wunderlin, and Duncan & Kartesz). Since there are herbarium specimens of noncultivated plants that apparently occurred beyond places of former cultivation (e.g., *Arnold s. n.*, Gainesville, Alachua County, Florida (FLAS); *Ellis s. n.*, Miami, Dade County, Florida (FLAS); *Brumbach 9506*, Sanibel Island, Lee County, Florida (FTG, GA, NY); *Cuthbert s. n.*, St. Helena Island, Beaufort County, South Carolina (FLAS); *Deramus D970*, Dauphin Island, Mobile County, Alabama (UNA, NCU, MO)), it is considered part of the flora. There are other collections from South Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana that were not reported to be of cultivated plants. Some of these probably also represent naturalized populations.

(Kinman & Martin). It arrived in the United States through slave routes from Africa (Weiss). Areas suitable for sorghum and dry-land cotton in the United States are considered suitable for nonirrigated cultivation of sesame (Weiss). It has been cultivated also in the southwestern United States.

With the exception of a few 19th century authors who considered *Ceratotheca* a section of *Sesamum*, *Sesamum* has been and is treated as a genus separated from others in the family by its unappendaged, nonwoody capsules. Within *Sesamum*, species are distinguished by presence and nature of wings, fringes, or other outer seed coat emergences and their patterns (unwinged, inconspicuously fringed, and almost always otherwise unadorned in *S. orientale*), leaf shape (very variable in *S. orientale*), persistence of calyx in fruit (persisting in *S. orientale*), habit (erect in *S. orientale*), degree of prominence of the lower lip of the corolla (slight in specimens of *S. orientale* from the southeastern United States), degree of reduction of the bracts subtending extrafloral nectaries (not very reduced in *S. orientale*), indumentum, and size and shape of capsules. Bruce (1953a) reviewed the history of classification within *Sesamum* and other genera of Pedaliaceae and expressed doubt about the validity of the then existing arrangement of sections of *Sesamum*, foreshadowing the recent revision of the genus (Grabow-Seidensticker, 1973, 1988; Ihlenfeldt & Grabow-Seidensticker).

In the most recent revision (Ihlenfeldt & Grabow-Seidensticker), *Sesamum* is divided into four sections, sect. SESAMOPTERIS Endl. (pollen 6 colpate, seeds 3 winged, testa foveolate), including *S. alatum* Thonn., *S. capense* Burman f., *S. grandiflorum* Schinz, and other species; sect. CHAMAESESAMUM Bentham (pollen 9–11 colpate, seeds unwinged and obscurely fringed, testa reticulate-foveate), including only *S. prostratum* Retz.; sect. APTERA Seidenst. (pollen 7–9 colpate, seeds unwinged and doubly fringed, testa patterns various but never foveolate), including *S. angolense* Welw., *S. calycinum* Welw., *S. radiatum* Schum. & Thonn., and other species; and sect. SESAMUM (pollen 9–10 colpate, seeds unwinged and doubly fringed, testa reticulate to smooth), including *S. latifolium* J. Gillett, *S. orientale*, and other species.

Section SESAMOPTERIS, species of which have winged seeds, is purportedly the most primitive section. It occurs only in Africa, and $2n = 26$ (20 "short," 6 "long" chromosomes) in all species. Section CHAMAESESAMUM is limited to Asia, and $2n = 32$ (all "short" chromosomes) in the only species. Section APTERA is represented only in Africa; its species are $2n = 32$ or 64 (all "short" chromosomes). Species of sect. SESAMUM occur in Africa and Asia; these species have $2n = 26$ or 32 (all "short" chromosomes).

Ihlenfeldt & Grabow-Seidensticker noted close relationships among *Sesamum*, *Ceratotheca* Endl., and *Dicerocaryum* Bojer. Of these genera, only *Sesamum* is divided into sections. *Sesamum* sect. *Chamaesesamum* is portrayed as more closely related to *Dicerocaryum* than to the other three sections of *Sesamum*, with the suggestion that sect.

Chamaesesamum may merit generic rank. *Sesamum* sect. *Aptera* is portrayed as closely related to *Ceratotheca*. Their innovative scheme also proposes that *Sesamum* sect. *Sesamum* is probably approximately equally closely related to *Sesamum* sects. *Aptera* and *Sesamopteris*. Evidence of the close relationships among these genera includes 1) overall morphological similarity, 2) pollen in *Ceratotheca* species spans the range of variation between the *Ceratotheca* and *Sesamum* types (discussed under *Ceratotheca*), and 3) the production of a sterile hybrid between *C. sesamoides* Endl. and *S. orientale* (Van Rheenen). In this context Hooker's opinion that *Ceratotheca* is only a section of *Sesamum* is noteworthy. To broaden the perspective on these affinities, it may be noted that a sterile hybrid was earlier reported between an unidentified species of *Sesamum* (*S. orientale*?) and *Martynia annua* L. (Martyniaceae) (Srinivasan, p. 162).

The two *Sesamum* species that occur in all three areas of the distribution of the genus, *S. Schenckii* Ascherson (= *S. grandiflorum*?) and *S. capense*, are $2n = 26$, as is *S. orientale*. Attempts to cross *S. orientale* with *S. alatum* (= *S. capense*?), also $2n = 26$, and with *S. Schenckii* have sometimes produced viable F_1 progeny. Sterile hybrids have resulted from crosses between *S. orientale* and *S. prostratum* (Asian, $2n = 32$). The amphidiploid of this sterile hybrid, $n = 29$, obtained by colchicine treatment of the F_1 , is stable and almost pure breeding (Tribe). It can be crossed with *Ceratotheca sesamoides*, yielding sterile progeny. Overall, about two-thirds of the attempted interspecific crosses in *Sesamum*, including crosses between species in different sections, have proved at least somewhat successful (Nayar).

Opinion is divided whether cultivated sesame originated in Africa or Asia. *Sesamum latifolium*, which Ihlenfeldt & Grabow-Seidensticker cited as the probable ancestor, occurs in Africa. The "wild gingelly of Malabar," a variant of *S. orientale* which Bedigian, Seigler, & Harlan cited as the probable ancestor, occurs in Asia, a secondary center of diversity of the genus. Other species put forth as possible contributors to the gene pool of cultivated sesame include *S. radiatum*, *S. prostratum*, *S. alatum*, and *Ceratotheca sesamoides*. The higher chromosome numbers ($2n = 32$ or 64) of all the above, except *S. alatum* and *S. orientale*, make them unlikely as progenitors (Nayar & Mehra). However, at least one Indian cultivar of *S. orientale* has six "B" chromosomes in addition to the normal complement of 26, and a loss of six chromosomes from earlier stock(s) may be involved in the domestication of cultivated sesame (Ihlenfeldt & Grabow-Seidensticker). It is possible that sesame was brought into cultivation independently from wild plants in both Africa and Asia. Although most *Sesamum* species occur in only one geographic region (e.g., Africa, Asia, or the East Indies), three species occur in both Africa and the East Indies, two in Africa, India, and the East Indies, and one in Africa and Sri Lanka (Nayar & Mehra).

A high frequency of secondary association of chromosomes occurs during metaphase I of meiosis in pollen mother cells of *Sesamum orientale* and other *Sesamum* species (Kobayashi & Shimamura, Ihlenfeldt & Grabow-Seidensticker, and others), suggesting a paleopolyploid origin for these species. The original ancestor of sesame has been postulated to have had $x = 7, 8, \text{ or } 9$ (Nayar & Mehra), depending on particular patterns of secondary association.

The above findings, especially the "B" chromosomes reported by Ihlenfeldt & Grabow-Seidensticker, seem to suggest that the *Sesamum* species with $2n = 32$ are paleotetraploids of the base number 8, and those with $2n = 26$ may be derived from $2n = 32$ by reduction, rather than $2n = 2x = 26$ from a base number of 13. Although earlier literature indicated both eight and thirteen as base numbers in *Sesamum* (Nayar) and the Pedaliaceae (Raven), more recent detailed study led Ihlenfeldt & Grabow-Seidensticker to consider eight to be the only base chromosome number for Pedaliaceae.

Sesamum species tend to prefer relatively dry areas in the warm regions where they are indigenous, although *S. radiatum* has been reported to occupy more moist habitats than *S. orientale* in Sri Lanka (Theobald & Grupe). *Sesamum orientale* is usually grown in areas with ca. 500–1100 mm annual rainfall between 25° North and 25° South latitudes. Variants are often adapted to local conditions to the extent that they do not do well when planted elsewhere. Among commercial crops, sesame is relatively tolerant of drought and poor soils, but it is sensitive to high salt concentrations and to excess moisture, especially at the seedling stage, when it is also vulnerable to competition from weeds. Plant growth in sesame has been found to be stimulated by infection with vesicular-arbuscular mycorrhizal fungi, indicating that these associations are important in obtaining nutrients, at least in some cultivars (Sulochana *et al.*). Sesame is intolerant of acid soils (Tribe). Sesame is very sensitive to day length; both long- and short-day forms occur (Purseglove), although it is reported to be basically a short-day plant (Weiss). On the basis of herbarium label data, flowering of noncultivated plants in the southeastern United States occurs at least from July through October.

Floral anatomy and development have been investigated in *Sesamum orientale* (Baillon, 1862; Singh, 1960b) and *S. alatum* (Sundari *et al.*), and leaf and hair anatomy have been studied in *S. laciniatum* J. T. Klein ex Willd. (Sayeedud-Din). The floral vasculature is noteworthy in that the primary vascular traces do not divide into calyx, corolla, or androecial traces, and in that the patterns are different between species. In *S. orientale*, the vasculature of the androecium and that of the median calyx bundles have a common origin; the calyx laterals and corolla vasculature arise as common traces; and the vasculature to the disc is partly from the traces to the stamens. In *S. alatum*, neither the disc nor the calyx vasculature has a trace in common with that to the androecium, but the petal midrib traces and sepal laterals have a common origin. In the adjacent abortive flowers (extrafloral nectaries)

of *S. orientale*, the vasculature is similar to but reduced from that of the fully developing flowers.

Pollen of *Sesamum orientale* usually has 9 or 10 colpi, but the number varies from 8 to 13. Other species tend to have fewer colpi and pollen that is either the same size or smaller (Straka & Ihlenfeldt). In *S. orientale*, the grains are normally trinucleate at anther dehiscence and have a papillose exine (Singh, 1960b).

Sesamum orientale is usually self pollinated (McGregor), although *Sesamum* flowers are of a type usually associated with bee pollination (Vogel). Significant but usually less than 10 percent cross pollination also occurs in cultivation. This is attributed to honey bees, which are often seen visiting sesame plants (Langham, 1944; McGregor). The bees alight on the lip of the flower, squeeze inside, and emerge with pollen on their bodies and in their pollen baskets. Small flies also occasionally visit sesame flowers. Despite sesame's being normally self-pollinated, heterosis has been reported repeatedly (Srivastava & Singh, Sodani & Bhatnagar, and earlier workers referenced in Brar & Ahuja). The flowers vary from white to pink or purple with various patterns of other colors, including dots, flakes, and smears, at various locations and intensities on the corolla (Langham, 1947a), all suggesting generalized attraction of insects. Pollen is usually shed from the longitudinally dehiscent anthers either before the flowers open (Purseglove) or shortly thereafter (Weiss). In early morning, when the flowers open, the bilobed stigma separates and is covered with pollen. After midday the flowers wilt and the corolla and stamens are usually shed in the evening of the same day. The stigma is receptive one day before flower opening or at least at the time of flower opening, and remains receptive for an additional day. Under experimental conditions, pollen germination begins 5 min after pollination and is mostly complete after 15 min. Pollen tubes begin to reach the base of the non-hollow style after 2 hours, the average rate of travel being 4.7 cm per hour. A small amount of germination and growth of pollen and tubes still goes on 24 hours after pollination (Yang & Chou). In the United States sesame usually flowers in midsummer when little else does, providing an opportunity to bee keepers. Sesame is often found as a relic of cultivation worldwide, and its tendency is to persist weakly in disturbed areas of the United States and elsewhere, including Madagascar (Humbert, 1962, 1971) and India (Gandhi). Perhaps paucity of reliable pollinators during time of flowering where it has been introduced explains this tendency in part.

Cleistogamy has been reported as a rare event in *Sesamum orientale*. Although such cleistogamous flowers were shown to be fertile when pollen from "sister plants" was used, some of the ovules in some of the resulting fruits were replaced by parenchymatous outgrowths bearing glandular hairs (Srivastava, 1954).

Embryogeny is of the Onagrad (Singh, 1960b) variation of the Crucifer type (Hanawa, 1953; Davis) in which the first division of the hypophysis initial takes place by a curved wall.

Endosperm is present in the seeds, contrary to statements in some of the early literature. It is cellular, oily, two to five cell layers thick, and terminal cells at both micropylar and chalazal ends are absorptive in function (Srinivasan, Davis). Oil drops are located in the cells of the cotyledons, as well as those of the endosperm (Vaughan). The endosperm is largely used up by the embryo in mature seeds. The embryo is straight and the cotyledons are prominent. The testa can be as thick as 16 cells. In mature seeds the outer epidermis is one layer thick. This layer bears clusters of calcium oxalate crystals in the outer half (*Sesamum orientale*) or inner half (*S. radiatum*). Ridges on seeds, when present, are caused by cell elongation.

The thin seed coat of *Sesamum orientale* has been selected for and represents a juvenile stage in seed ontogeny, although vestiges of patterns reminiscent of those of other species occasionally occur, including the specimen in which six "B" chromosomes were documented. Moreover, the light color of the seed coat reflects the absence of tannins normally deposited in the testa during late stages of seed ontogeny (Ihlenfeldt & Grabow-Seidensticker). In many species of *Sesamum*, seeds are darkly colored when ripe (Ihlenfeldt & Grabow-Seidensticker).

Miscellaneous compounds have been reported from *Sesamum*, including alcohols, sugars, flavones, furanoflavones, lignans, and others (Hegnauer, Gibbs). Sesame seeds contain the lignans sesamin and sesamol, which have not been reported from other edible oils (Bedigian, Seigler, & Harlan). Although these compounds have also been found in various tissues of members of related families, they seem not to be present in either *S. alatum* or *S. capense* and are not always detected in members of related families. Sesamol, another lignan, has also been isolated from the seeds of *S. orientale*. Some compounds in the seed oil of *S. orientale* may be toxic or may cause tumors (Bedigian, Seigler, & Harlan). *Sesamum orientale* tested negative for cyanogenesis (Gibbs). Two new antifungal naphthoxirene derivatives and a new iridoid glucoside have been isolated recently from the root bark of *S. angolense* by Potterat *et al.* (1987, 1988).

Yields of sesame are traditionally low compared to other oilseed crops, but a potential of up to a ton per acre per year has been demonstrated (McGregor). In 1976 sesame was reported to rank ninth worldwide among vegetable oil crops (Nayar). World production has recently remained static, though commercial demand has declined (Weiss).

Much experimental work has been done in attempts to improve sesame as a commercial crop (reviewed in Brar & Ahuja, Weiss, and others), contributing basic as well as practical knowledge. It is a convenient organism for genetic research (Langham, 1948), and many mutants have been found that are phenotypically expressed. These mutants include tufts of hair, glabrosity, separate corolla lobes, double flowers or lips, and fused anthers (Langham, 1946a). Genetically based variations in flower color have been classified as basic factors (which themselves do not add color but rather inhibit expression of factors controlling "true" color factors); as color factors (the coloring visible if

basic factors are present); as pattern factors (location of color); and as intensification factors (amount of coloring matter) (Langham, 1947a). Simple Mendelian ratios have been found for most vegetative, floral, fruit, and seed characters, but duplicate, modifying, and complementary factors, multiple alleles, and linkages have also been demonstrated. Controls of some phenotypic characters are provisionally assigned to genes on each of the 13 chromosome pairs by Nohara (1934). High heritability values and few controlling genes have been postulated for percentages of germ, protein, and oil in sesame seeds (Culp, 1959).

Cultivars with indehiscent capsules and cultivars with extra flowers per node or extra carpels (up to 12) per fruit have been developed and tested for commercial potential with some but not spectacular success, as have cultivars with fruits that mature simultaneously rather than acropetally on the plant. A single cultivated plant can produce several thousand seeds.

Tetraploid variants have been induced with colchicine and studied experimentally for possible commercial value. The embryo grows more slowly in early stages in tetraploid plants, but development later catches up with that of diploids (Hanawa, 1953). Flowering is slightly later in tetraploids. Although fertility is somewhat reduced in tetraploids, pollen fertility is still nearly equal to that in diploids. Sesame polyploids characteristically are more variable than diploids. They also have more branching, larger and thicker stems and leaves, simple rather than tripartite leaves, and larger but fewer stomata than diploids. Pollen grains, flowers, fruits, and seeds usually are larger, and there are more capsules than in diploids. However, there are fewer seeds per capsule and usually per plant in tetraploids, so oil yield is not increased (Kobayashi & Shimamura; Srivastava, 1956).

The economically most important product of *Sesamum orientale* is its seed oil, although seed rather than oil is traded in world markets. The oil is in demand because of its good taste, stability, and lack of tendency to become rancid even without refrigeration, owing to its resistance to oxidation. It is odorless. Seed oil content is usually ca. 50 percent, but it varies with the source of the plants. Palmitic, stearic, oleic (ca. 40 percent), and linoleic (ca. 40 percent) acids are reported to be the major fatty acids present. Linolenic acid is absent. About 14 percent of the acids are saturated. The oil from both raw and toasted seeds is used in cooking and on salads. Oil from raw seeds is also used in margarine, soap, and paints, and as a lubricant and illuminant. In India, sesame oil is used as a body oil, and in the Philippines, it is used as an antirheumatic in massage treatment. It is a solvent vehicle for pharmaceutical drugs, perfumes, shampoos, and cosmetics, and is a component of some liniments and ointments.

Whole seeds are also commercially important, although less so than the oil. These are used on bread products. The seeds are used in soups, other foods, and medicines, e.g., as a laxative, in India, Africa, and Latin America. Protein content is ca. 20–25 percent and water content ca. 5 percent. The protein chemistry of the seeds has been

well studied (e.g., Rajendran & Prakash). Wide ranges in content of iron and other mineral constituents of sesame seeds have been reported (e.g., Brar & Ahuja; Friedlander; Khan *et al.*). A large percentage of the mineral content is in the hulls of the seeds, which are usually removed before commercial use.

Among Indian oilseed flours including soya (*Glycine* L.), groundnut (*Arachis* L.), and chickpea (*Cicer* L.), sesame contains above average quantities of fat, crude fiber, calcium, phosphorus, iron, and thiamine. Compared to soya, cottonseed (*Gossypium* L.), and groundnut flours, sesame flour is high in methionine and tryptophan (Weiss). Sesame meal and expressed cake are high in methionine (in which legumes are deficient) and are thus valuable food and feed supplements for humans and livestock. The expressed cake is also high in protein, though it may be low in lysine.

Sesame also is a main ingredient of halvah (a Middle Eastern confection) and tahini (sesame paste). Young leaves are used in soups. The leaves have various medicinal uses in Africa, including the use of the mucilage from sesame plants in the treatment of diarrhea and dysentery. The cake has been used as a hair dressing and in rituals in Sudan. Sesame meal is a meat substitute and filler. Sesamin, sesamol, and sesamolins from the seeds are synergists for pyrethrin insecticides. Antifungal activity has been demonstrated in extracts from leaves, fruits, and seeds of sesame at various plant ages (Pagnocca *et al.*). Cherokee Indians have used the seed oil as a cathartic and a decoction of the leaves and seeds as an antidiarrheal, gynecological, and pediatric aid (Hamel & Chiltoskey, Moerman). Sesame is sometimes grown in the United States for use as a component of birdseed.

Other species of *Sesamum* have been used in some of the same ways as *S. orientale* on a more local basis, most often in Africa but also in Asia and Latin America (Uphof). *Sesamum angolense* has several African traditional medicinal uses. One of the new antifungal naphthoxirene derivatives recently isolated from its root bark was toxic to human colon carcinoma cells (Potterat *et al.*, 1987).

Seedling shoot-tips with cotyledons can be multiplied through tissue culture in *Sesamum orientale*. This could be a first step toward creating useful variants of sesame by cell culture, which has already been accomplished in some other crops (George *et al.*).

Sesamum orientale is subject to attack by a number of insect pests, reducing yield worldwide by ca. 25 percent. Fungal and bacterial diseases are common, and viral and other diseases and malformations also occur (thorough review by Weiss). The problems are locally defined, but according to Purseglove the most serious diseases are leaf-spots and *Fusarium* wilt. Some pests eat seeds, some leaves. Attacks can occur in the field or in storage. Leaf-curl disease, caused by a virus, was found to reduce plant yield and seed oil content but, at least on a percentage basis, to increase seed protein content (Prasad *et al.*).

REFERENCES:

The following citations have been selected from an extensive bibliography dealing with various aspects of *Sesamum*. Because of sesame's commercial importance, the literature on it is voluminous. This literature has been reviewed by various authors. Articles noted below as review articles and those noted as having extensive bibliographies are suggested as sources of much additional information and many more references on sesame; additional citations will also be found in most other references cited below.

Under family references see ABELS; ALVARADO; BACKER; BACKER & BAKHUIZEN VAN DEN BRINK; BAILEY; BAILEY *et al.*; BAILLON; BATSON; BEDIGIAN, SEIGLER, & HARLAN; BENTHAM & HOOKER; BERNHARDI; BOLKHOVSKIKH *et al.*; BRUCE, 1953a, b; DE CANDOLLE; CARLQUIST; CLARKE; CLEWELL; COOKE; CORNER; DAVIS; DIELS; DUNCAN & KARTESZ; ERDTMAN; GIBBS; HEGNAUER; HEINE; HOOKER; HUMBERT, 1962, 1971; HUTCHINSON; IHLENFELDT, 1965, 1967b, 1988; LE MAOUT & DECAISNE; LONG & LAKELA; MACROBERTS; MATTHEW & RANI; MELCHIOR; METCALFE & CHALK; MEISNER; MONOD; NETOLITZKY; PAL & PARIA; PURSEGLOVE; RADFORD *et al.*; RAO; VAN RHEENEN; ROTH; ROXBURGH; SAYEEDUD-DIN; SCHNARF; SINGH, 1958, 1960a, b; SMALL, 1913, 1933; SOLEREDER; SRINIVASAN; STAPF, 1895, 1906; STOPP; STRAKA; STRAKA & IHLENFELDT; THEOBALD & GRUPE; UPHOF; VOGEL; WELWITSCH; and WUNDERLIN.

ALY, H. Y., M. A. KARARAH, & G. A. BEAN. Mycoflora associated with some oil crops during storage and their control. (Abstr.) *Phytopathology* 76: 562. 1986. [Incl. sesame; carbon tetrachloride treatment effective.]

ASHRI, A., & D. PAVEVITCH. *Exper. Agr.* 15: 81. 1979.* [Seed dormancy.]

BAILLON, H. Organogénie florale du sésame. *Adansonia* 2: 1-4. 1862.

BEDIGIAN, D., & J. R. HARLAN. Nuba agriculture and ethnobotany, with particular reference to sesame and sorghum. *Econ. Bot.* 37: 384-395. 1983. [Sesame in a small geographical area has much variation, which correlates with both cultural and microenvironmental factors.]

— & —. Evidence for cultivation of sesame in the ancient world. *Ibid.* 40: 137-154. 1986. [Extensive bibliography; incl. linguistic sources.]

—, A. SMYTH, & J. R. HARLAN. Patterns of morphological variation in *Sesamum indicum*. *Ibid.* 353-365. [Factor, discriminant, and cluster analyses of otherwise apparently continuous morphological variation confirmed visual impressions of distinctiveness of tetracarpellate plants and geographical variants.]

BRAR, G. S., & K. L. AHUJA. Sesame: Its culture, genetics, breeding and biochemistry. *Ann. Rev. Pl. Sci.* 1: 245-313. 1979. [Extensive review and bibliography.]

BRITTON, N. L., & P. WILSON. Botany of Porto Rico and the Virgin Islands. Myrtales to Lycopodiales. In: *Scientific survey of Porto Rico and the Virgin Islands* 6. vi + 664 pp. New York. 1925. [Pedaliaceae, 201, 202; only *S. orientale*.]

BROWN, W. H. Minor products of Philippine forests. Vol. 3. i + 329 pp. Manila. 1921. [*S. orientale*, 236, 237.]

—. Useful plants of the Philippines. Vol. 3. 507 pp. Manila. 1957. [*S. orientale*, 329-333; incl. vernacular names.]

CANDOLLE, A. P. DE. Plantes rares du jardin de Genève. vi + 93 pp. Geneva. 1829. [*S. indicum*, 15-20, pl. 5; suggests combining *S. indicum* with *S. orientale*, but does not.]

CHAKRAVARTI, S. C., & B. K. ARORA. Experimental induction of leaf heteromorphism in *Sesamum indicum* L. *Curr. Sci. Bangalore* 27: 32. 1958. [By removal of cotyledonary leaves and shoot apices soon after germination.]

CHANDRAMONY, D., & N. K. NAYAR. Genetic variability in sesamum. *Indian Jour. Agr. Sci.* 55: 769, 770. 1985. [Experiments with *S. orientale* cultivars to assess

phenotypic, genotypic, and environmental variation in ten characters related to yield.]

- CULP, T. W. Inheritance and association of oil and protein content and seed coat type in sesame, *Sesamum indicum* L. *Genetics* **44**: 897-909. 1959. [High heritability values for percent germ, protein, and oil, involving few genes per character.]
- . Inheritance of plant height and capsule length in sesame, *Sesamum indicum* L. *Agron. Jour.* **52**: 101-103. 1960. [Controlled by 3-10 and 2-5 pairs of genes, respectively; dominance varied from cross to cross.]
- D'ARCY, W. G. Flora of Panama. Family 173. Pedaliaceae. *Ann. Missouri Bot. Gard.* **67**: 1057-1059. 1980. [Only *S. orientale*.]
- DE WILDEMAN, É. Decades novarum specierum Florae Congolensis 3. *Bull. Jard. Bot. Bruxelles* **5**: 1-108. 1915. [*S. biapiculatum* De Wild. (= *S. radiatum* Schum. & Thonn.), with two beaks at the apex, 58, 59.]
- FERNALD, M. L. Gray's manual of botany, ed. 8. lxiv + 1632 pp. New York *et al.* 1950. [*S. orientale*, 1302; sporadic in waste ground, rarely persistent.]
- FRIEDLANDER, B. The secrets of the seed vegetables, fruits, and nuts. xvi + 287 pp. New York. 1974. [Sesame, 173, 174, 262, 266; constituents of seeds.]
- FUKUDA, Y., T. OSAWA, M. NAMIKI, & T. OZAKI. Studies on antioxidative substances in sesame seed. *Agr. Biol. Chem.* **49**: 301-306. 1985. [Chemical identifications and activities of extracts.]
- GAERTNER, J. Fructibus et seminibus plantarum. Vol. 2. lii + 520 pp. + pls. 80-180. Stuttgart. 1791. [*Sesamum*, 132, pl. 110.]
- GANDHI, K. N. In: C. J. SALDANHA & D. H. NICOLSON, eds., Fl. Hassan District, Karnatka, India. viii + 915 pp. New Delhi and Washington. 1976. [*Sesamum*, 562.]
- GEORGE, L., V. A. BAPAT, & P. S. RAO. In vitro multiplication of sesame (*Sesamum indicum*) through tissue culture. *Ann. Bot.* **II**. **60**: 17-21. 1987.
- GOLDBLATT, P., ed. Index to plant chromosome numbers 1982-1983. *Monogr. Syst. Bot. Missouri Bot. Gard.* **viii** + 224 pp. 1985. [*Sesamum*, 144.]
- , ed. Index to plant chromosome numbers 1984-1985. *Ibid.* **ix** + 264 pp. St. Louis. 1988. [*Sesamum*, 159].
- & D. E. JOHNSON, eds. Index to plant chromosome numbers 1986-1987. *Ibid.* **ix** + 243 pp. St. Louis. 1990. [*Sesamum*, 138].
- GRABOW-SEIDENSTICKER, U. Monographie der Gattung *Sesamum* L. (Pedaliaceae, R. Br.). Hamburg. 1973.*
- . The *Sesamum calycinum* complex (Pedaliaceae R. Br.). *Mitt. Inst. Allg. Bot. Hamburg* **22**: 217-241. 1988. [Taxonomic revision and evolutionary and phylogenetic analyses of several species of *Sesamum* sect. *Aptera* Seidenst., a group possibly with an ancestor common to species in the complex and to sesame and *Ceratotheca*.]
- GRAHAM, J. A catalogue of the plants growing in Bombay and its vicinity. iv + 254 + ix pp. Bombay. 1839. [Pedalineae, 126, 127; *S. indicum* L. in synonymy with *S. orientale*; see ROXBURGH (under family treatment) for an earlier combination of these two species.]
- HAMEL, P. B., & M. V. CHILTOSKEY. Cherokee plants. *Sylva*, North Carolina. 1975.* [*S. orientale*, medicinal uses.]
- HANAWA, J. The embryo sac formation and the embryogeny of *Sesamum indicum* L. in the diploid and the tetraploid strains. *Bot. Mag. Tokyo* **66**: 98-102. 1953.
- . Leaf development following longitudinal split of the shoot apices of the germinating embryo and the seedling in *Sesamum indicum* L. *Ibid.* **72**: 425-431. 1959. [Lateral fusion of leaves that would normally be opposite and separate.]
- . Late embryogeny and histogenesis in *Sesamum indicum* L. *Ibid.* **73**: 369-376. 1960.

- . Further studies on the double-leaf formation in *Sesamum indicum* L. *Ibid.* **74**: 402–413. 1961.
- HATANAKA, S. I. Oligosaccharides in the seeds of *Sesamum indicum* L. *Arch. Biochem. Biophys.* **82**: 188–194. 1959. [Possible new isomer of lychnose.]
- HEDRICK, U. P. Sturtevant's edible plants of the world. viii + 686 pp. New York. 1919, republished 1972. [Sesame, 531, 532.]
- HENRY, A., & H. S. DAULAY. Genotype-environment interactions for seed yield in *Sesamum*. *Indian Jour. Agr. Sci.* **57**: 622–624. 1987. [Cultivars vary in responses to environmental variations.]
- HILTEBRANDT, V. M. Sesame (*Sesamum indicum* L.). *Bull. Appl. Bot. Genet. Pl. Breed.* **9**: 1–114. 1932.*
- IHLENFELDT, H.-D., & U. GRABOW-SEIDENSTICKER. The genus *Sesamum* L. and the origin of the cultivated sesame. Pp. 53–60 in G. KUNKEL, ed., *Taxonomic aspects of African economic botany*. Proc. IX Plenary Meeting of AETFAT. 250 pp. Las Palmas de Gran Canaria. 1979. [Subdivision of *Sesamum* into four sections (*Sesamum*, *Sesamopteris*, *Chamaesesameum*, and *Aptera*) with discussion of characters, including cytology; *Ceratotheca*, 55.]
- IKUSE, M. Pollen grains of Japan. xii + 303 pp. Tokyo. 1956. [Polar view, *Sesamum orientale*, pl. 65.]
- IWANAMI, Y., T. SASAKUMA, & Y. YAMADA. Pollen: Illustrations and scanning electron micrographs. viii + 198 pp. Tokyo. 1988. [Equatorial view of prolate grain of *Sesamum orientale*, 91.]
- JOHN, C. M., G. V. NARAYANA, & C. R. SESHADRI. The wild gingelly of Malabar. *Madras Agr. Jour.* **37**: 47–50. 1950.* [One of the putative progenitors of cultivated sesame.]
- JOSHI, A. B. *Sesamum*. A monograph. Hyderabad. 1961.* [Cytogenetics and other matters; published by Central Oil Seeds Committee, more recently the Indian Council of Agricultural Research, New Delhi.]
- KEDHARNATH, S., S. RAMANUJAM, & A. B. JOSHI. Chromosome pairing in two sesquiploid hybrids and its bearing on genome relationship in the genus *Sesamum*. *Indian Jour. Genet. Pl. Breed.* **19**: 201–209. 1969.*
- KHAN, H. H., N. BIBI, & G. M. ZIA. Trace metal contents of common spices. *Pakistan Jour. Sci. Industr. Res.* **28**: 234–237. 1985. [Sesame comparatively low in iron, zinc, manganese, chromium, nickel, and cobalt, comparatively high in copper.]
- KHIDIR, M. O. Genetic studies in sesame. II. Inheritance of flower colour and number of locules per pod. *Exper. Agr.* **9**: 361–364. 1973.*
- KHULLAR, S., M. M. SIMOT, & G. C. NANAWATI. Effect of seed treatment with α -amylase on the biometry of the sesame plant and on biochemical composition of seeds. *Curr. Sci. Bangalore* **55**: 129–132. 1986. [Soaking in low concentrations before sowing promotes increased yield; high concentrations usually had the opposite effects.]
- KINMAN, M. L. Utilization abstract. *Sesame*. *Econ. Bot.* **9**: 150. 1955.
- & J. A. MARTIN. Present status of sesame breeding in the United States. *Agron. Jour.* **46**: 24–27. 1954. [Review article.]
- KOBAYASHI, T. J., & T. SHIMAMURA. Morphological and cytological studies on induced polyploidy in *Sesamum indicum* L. *Jap. Jour. Genet.* **27**: 157–171. 1952. [Colchicine treatment methods, characteristics of tetraploids, and secondary chromosome associations.]
- KULKARNI, R. S., S. SHIVASHANKAR, D. M. MAHISHI, & P. M. SALIMATH. Multivariate analysis of divergence in a world collection of *Sesamum indicum*. (Abstr.) *Int. Bot. Congr. Abstr.* **17**: 290. 1987. [Two main groups of genotypes distinguished; factor analyses showed reproductive traits tend to be more important than developmental ones.]
- KUMAR, L. S. S., & A. ABRAHAM. A cytological study of sterility in *Sesamum orientale* L. *Indian Jour. Genet.* **1**: 41–60. 1941.*

- LANGHAM, D. G. Natural and controlled pollination in sesame. *Jour. Hered.* **35**: 254–256. 1944. [Cross pollination 4.6 percent, attributed mostly to honey bees and occasionally to flies; progeny of glabrous recessive mutants used as indicators.]
- . Genetics of sesame. *Ibid.* **36**: 135–142. 1945a. [Mutants for glabrous leaves and number of foliar glands inherited complexly; tetracarpellate fruit mutant correlates with lack of glands on dorsal leaf surfaces; number of capsules per node shows simple Mendelian inheritance; photographs of mucilage glands.]
- . Genetics of sesame II. Inheritance of seed pod number, aphid resistance, “yellow leaf,” and wrinkled leaves. *Ibid.* 245–253. 1945b. [By recessive genes, except aphid resistance more complex.]
- . Genetical studies of the sesame flower. *Science* **103**: 280. 1946a. [Enumeration and lists of some mutant types.]
- . Genetics of sesame III. “Open sesame” and mottled leaf. *Jour. Hered.* **37**: 149–152. 1946b. [Recessive indehiscent fruit mutant is semi-sterile because of curved styles.]
- . Genetics of sesame IV. Some genetic variations in the color of the sesame flower. *Ibid.* **38**: 221–224. 1947a. [Basic, color, pattern, and intensification factors studied for several generations of crosses.]
- . Initiation of a linkage map for sesame (*Sesamum indicum* L.). (Abstr.) *Genetics* **32**: 94. 1947b. [Over 100 characters mapped preliminarily; apparently not published in greater detail.]
- . Seedling characters in sesame (*Sesamum indicum* L.). (Abstr.) *Ibid.*: 94. 1947c. [List of characters, mostly single gene differences.]
- . Genetics of sesame. (Abstr.) Pp. 81, 82 in Eighth International Congress of Genetics, 7th–14th July 1948, Abstract book. 147 + vii pp. Stockholm. 1948. [Advantages of sesame for intensive genetic research.]
- LYON, K. C. Sesame: Current knowledge of composition and use. *Jour. Am. Oil Chem. Soc.* **49**: 245–249. 1972. [Review article.]
- MAHESWARI, P. An introduction to the embryology of angiosperms. x + 453 pp. New York. 1950. [*Sesamum*, 30, 31; anther epidermal cell walls become cutinized and lignified over the entire surface before dehiscence.]
- MARTIN, A. C. Comparative internal morphology of seeds. *Am. Midl. Nat.* **36**: 513–660. 1946. [*Sesamum*, 604, 605.]
- MASEFIELD, G. B., M. WALLIS, S. G. HARRISON, & B. E. NICHOLSON. The Oxford book of food plants. viii + 206 pp. Oxford. 1969, reprinted 1971. [*Sesamum*, 22, 23.]
- MCGREGOR, S. E. Insect pollination of cultivated crop plants. U.S. Dep. Agr. Agr. Res. Serv., Agr. Handbook **496**. viii + 411 pp. Washington. 1976. [Sesame, 334; self-pollinated or occasionally cross-pollinated by bees; more crossing when more bees present.]
- MERXMÜLLER, H. Über die Gattung *Sesamum* L. in Südwestafrika. *Mitt. Bot. Staatssam. München* **3**: 1–13. 1959.
- MOERMAN, D. E. Medicinal plants of native America. Vol. 1. xx + 534 pp. Ann Arbor, Michigan. 1986. [*Sesamum*, 451; Cherokee uses.]
- MORETI, A. C. D. C. C., L. C. MARCHINI, & M. A. B. REGITANO-DARCE. Observations of entomophilic pollination of sesame *Sesamum indicum* L. *Anais Soc. Entomol. Brasil* **17**: 127–134. 1988.*
- MORTON, J. F. Atlas of medicinal plants of Middle America: Bahamas to Yucatan. xxviii + 1420 pp. Springfield, Illinois. 1981. [*S. orientale*, 835; incl. many vernacular names and reported uses.]
- MUKHERJEE, S. Chromosome type of *Sesamum orientale* L. *Indian Oilseed Jour.* **3**: 41, 42. 1959.*
- MURTY, B. R., & F. OROPEZA. Diversity pattern in *Sesamum* mutants selected for a semi-arid cropping system. *Theor. Appl. Genet.* **77**: 275–286. 1989.*

- MURTY, G. S. S. Inheritance of three new mutants in sesame. *Curr. Sci. Bangalore* **57**: 204–206. 1988. [Distinct from similar mutants reported elsewhere, including a flower color pattern mutant.]
- NAYAR, N. M. *In*: N. W. SIMMONDS, ed., *Evolution of crop plants*. xii + 339 pp. London and New York. 1976. [Sesame, 231–233.]
- & K. L. MEHRA. Sesame: Its uses, botany, cytogenetics, and origin. *Econ. Bot.* **24**: 20–31. 1970. [Review article, extensive bibliography.]
- NICOLSON, D. H., C. R. SURESH, & K. S. MANILAL. An interpretation of van Rheede's *Hortus Malabaricus*. *In*: W. GREUTER, ed., *Regnum Veg.* 119. 378 pp. Königstein. 1988. [Pre-Linnaean names attributed to particular plants; *S. orientale*, 207; DE CANDOLLE (1829) interpreted as having combined *S. orientale* and *S. indicum*.]
- NOHARA, S. Genetical studies on *Sesamum indicum* L. *Jour. Coll. Agr. Univ. Tokyo* **12**: 227–386. 1933. [Extensive study of characteristics of "brown," "white," and "black" sesame.]
- . Gametogenesis and embryogeny of *Sesamum indicum* L. *Ibid.* **13**: 9–25. 1934. [Genes controlling particular characters located on specific chromosomes.]
- OSMAN, H. E., & A. M. NOUR. Response of sesame varieties to environment in the Sudan central highlands. *Jour. Agr. Sci. Cambridge* **104**: 565–569. 1985. [Minority of varieties combined high yield and stability of performance.]
- PAGNOCCA, F. C., O. A. DA SILVA, M. J. HEBLING-BERALDO, & O. C. BUENO. Toxicity of sesame extracts to the symbiotic fungus of leaf-cutting ants. *Bull. Entomol. Res.* **80**: 349–352. 1990.
- POOLE, D. D. Aerial stem rot of sesame caused by *Helminthosporium sesami* in Texas. *Pl. Disease Rep.* **40**: 235. 1956.
- POTTERAT, O., J. D. MSONTHI, & K. HOSTETTMANN. Four iridoid glucosides and a phenylpropanoid glycoside from *Sesamum angolense*. *Phytochemistry* **27**: 2677–2679. 1988. [One iridoid glucoside a previously unreported compound.]
- , H. STOECKLI-EVANS, J. D. MSONTHI, & K. HOSTETTMANN. Two new antifungal naphthoxirene derivatives and their glucosides from *Sesamum angolense* Welw. *Helvet. Chim. Acta* **70**: 1551–1557. 1987. [One toxic to human carcinoma cells; *S. angolense* has several African traditional medicinal uses.]
- PRASAD, B., O. P. VERMA, & L. N. DAFTARI. Effect of leaf curl disease on seed and oil quality of sesame (*Sesamum indicum* L.). *Curr. Sci. Bangalore* **54**: 388, 389. 1985. [Yield and seed oil content reduced; seed protein percentage increased.]
- QUISUMBING, E. Medicinal plants of the Philippines. iv + 1262 pp. Quezon City. 1978. [Sesame, 879–881; Philippine vernacular names and uses for sesame.]
- RAGHAVAN, T. S., & K. V. KRISHNAMURTHY. Cytogenetical studies in *Sesamum*. I. *Proc. Indian Acad. Sci. B.* **26**: 236–275. 1947.*
- RAJENDRAN, S., & V. PRAKASH. Isolation and characterization of β -globulin low molecular weight protein fraction from sesame seed (*Sesamum indicum* L.). *Jour. Agr. Food Chem.* **36**: 269–275. 1988.
- RAMAKRISHNAN, C. V., & B. N. BANERJEE. Studies on mold lipase; comparative study of lipases obtained from molds grown on *Sesamum indicum*. *Arch. Biochem. Biophys.* **37**: 131–135. 1952.
- RAMANATHAN, K. A note on the interspecific hybridization in *Sesamum*. *Madras Agr. Jour.* **37**: 397–400. 1950.*
- RAMANUJAM, S., & A. B. JOSHI. Chromosome number of *Sesamum laciniatum* Klein. *Nature* **161**: 99, 100. 1948. [$2n = 32$.]
- RHEENEN, H. A. VAN. Natural cross-fertilization in sesame (*Sesamum indicum* L.). *Trop. Agr. Trinidad* **45**: 147–153. 1968.*
- RHIND, D., & U. B. THEIN. The classification of Burmese sesamums (*Sesamum orientale* Linn.). *Indian Jour. Agr. Sci.* **3**: 478–495. 1933. [Descriptions of

intraspecific variation in cultivars; incl. association of characters with each other.]

- SEEGELER, C. J. P. *Sesamum orientale* L. (Pedaliaceae): Sesame's correct name. Taxon **38**: 656-659. 1989. [Affirmation that *S. indicum* is not the correct name; combination made seven years earlier than recently reported.]
- SIKKA, A., & A. GUPTA. Pollination studies in *Sesamum orientale* L. Indian Jour. Agr. Sci. **9**: 33-41. 1949.*
- SIMS, J. *Sesamum indicum*. Indian sesamum, or oily-grain. Bot. Mag. **41**: pl. 1688. [2 pp. text.] 1814.
- SIVANESAN, A. Teleomorphs of *Cercospora sesami* and *Cercoseptoria sesami*. Trans. Brit. Mycol. Soc. **85**: 397-404. 1985. [Descriptions of and keys to fungi causing leaf-spot diseases of sesame.]
- SODANI, S. N., & S. K. BHATNAGAR. Heterosis and inbreeding depression in sesame. Indian Jour. Genet. Pl. Breed. **50**: 87, 88. 1990.*
- SRIVASTAVA, D. P., & S. N. SINGH. Heterosis in sesame. Jour. Indian Bot. Soc. **47**: 79-88. 1968. [Despite being normally self-pollinated.]
- SRIVASTAVA, R. N. Cleistogamy in til (*Sesamum orientale* L.). Curr. Sci. Bangalore **23**: 268. 1954. [Description and reproductive behavior of cleistogamous plants.]
- . Production of fertile autotetraploids in sesame and their breeding behavior. Jour. Hered. **47**: 241-244. 1956. [Morphological and cytological characteristics also discussed.]
- STEENIS, C. G. G. J. VAN. Dedication—revisions addenda—index. Fl. Malesiana I. **7**. 18 pp. + 755-876. 1976. [Correction of sesame's name from *S. indicum* to *S. orientale*, 829.]
- SULOCHANA, T., C. MANOHARACHARY, & P. R. RAO. Growth response and root colonization in cultivars of sesame to VAM fungi. Curr. Sci. Bangalore **58**: 519, 520. 1989. [Enhanced plant growth.]
- SUNDARI, K. T., P. S. P. RAO, & L. L. NARAYANA. Floral anatomy of *Sesamum alatum* Thonn. Curr. Sci. Bangalore **49**: 752-754. 1980. [Glandular, papillose inner stigma lobe surface; incl. comparisons with *S. orientale*.]
- TAYLOR, K. R. Pedaliaceae. Fl. Veracruz **29**. 5 pp. 1983. [Only *S. orientale*.]
- TRIBE, A. J. Sesame. Field Crop Abstr. **20**: 189-194. 1967. [Review article, extensive bibliography.]
- TUTIN, T. G. *Sesamum* L. Fl. Europaea **3**: 284. 1972. [Only *S. orientale*.]
- VAIDEHI, B. K., & P. LALITHA. Fungal succession in *Sesamum indicum* seeds. Indian Jour. Bot. **8**: 39-48. 1985.*
- VAUGHAN, J. G. The structure and utilization of oil seeds. xvi + 279 pp. London. 1970. [*S. orientale*, *S. radiatum*, 200-203.]
- VIJAYALAKSHMI, M., & A. S. RAO. Vesicular-arbuscular mycorrhizal associations of *Sesamum*. Proc. Indian Acad. Sci. Pl. Sci. **98**: 55-59. 1988.
- WEISS, E. A. Oilseed crops. x + 660 pp. London and New York. 1983. [Incl. extensive review and bibliography for sesame.]
- YANG, C. Y., & C. CHOU. A study on the germination and growth of sesame (*Sesamum indicum* L.) pollen on the pistil. (In Chinese; Russian summary). Acta Bot. Sinica **12**: 211-219. 1964. [Most pollen germinates within 15 min after pollination; many pollen tubes enter ovules within four to six hours after pollination.]
- YEN, G.-C. Influence of seed roasting process on the changes in composition and quality of sesame (*Sesame* [sic] *indicum*) oil. Jour. Sci. Food Agr. **50**: 563-570. 1990. [Oils from unroasted seeds and from seeds roasted at different temperatures compared chemically and for flavor; 220° suggested as optimum roasting temperature.]
- YOUSIF, Y. H., F. T. BINGHAM, & D. M. YERMANOS. Growth, mineral composition, and seed oil of sesame (*Sesamum indicum* L.) as affected by boron and exchangeable sodium. Soil Sci. Soc. Am. Proc. **36**: 923-926. 1972. [Plant

growth reduced with increasing boron; yields reduced with 15 or more percent exchangeable sodium.]

2. *Ceratotheca* Endlicher, *Linnaea* 7: 5. 1832.

Annual or perennial herbs [or small shrubs] in pinelands and disturbed areas such as dry fields or roadsides [or in other relatively open areas]. Stems erect [or semi-prostrate], [branched or] unbranched, terete below, becoming \pm tetragonal, pubescent. Leaves usually drying light green or brown, and discolorous [or concolorous], opposite, subopposite, [or rarely alternate]; blades simple, unlobed to shallowly 3 lobed, shape broadly ovate-cordate to less often rounded, elliptical or slightly obovate, often varied within plants; apices acute to obtuse, bases cuneate, [truncate], rounded, or cordate, main lateral veins ca. 3–6 [–10]; margins usually crenate; blades [usually] pubescent. Flowers solitary, sometimes subtended by 1 or 2 rudimentary or linear bract(s), subcircular, reduced petiolate leaves, or rudimentary flower(s). Calyx lobes unequal, usually narrowly ovate, valvate or subvalvate, usually deciduous [or persistent] in fruit. Corolla [white, pink, or] purplish, lobes sometimes with darker stripes or lines of dark spots, subbilabiate, usually subhorizontal, the lowest lobe the longest; lobes entire. Staminode absent; pollen (6) 7–9 (10) colpate, suboblate to spheroidal, peroblate, or prolate. Carpels 2, locules 2. Fruits obovate, truncate or subtruncate at apex, with 2 usually subhorizontal [to suberect], narrowly triangular to linear horns at the outer edges of the apex, the horns early splitting in half longitudinally and then appearing to be 4. Seeds flattened, doubly [or singly] fringed, unwinged, tan to nearly black, flat surfaces [sometimes radially] rugose to verrucose. Endosperm cellular; embryo straight. Chromosome number $2n = 32$. (Including *Sporledera* Bernh. non Hampe.) TYPE SPECIES: *C. sesamoides* Endl. (Name from Greek *keratos*, horn, and *theke*, case, container, capsule, in reference to the fruit.)

A genus of five species of tropical and southern Africa. The southern African *Ceratotheca triloba* (Bernh.) Hooker f. has been introduced into the United States as a cultivated ornamental and has escaped to become naturalized in the high pinelands and roadsides of peninsular Florida (Small, 1933).⁴ The natural range of *C. triloba* is eastern

⁴Field observations are needed to evaluate the extent of persistence of *C. triloba* outside of cultivation. It is not mentioned by Clewell, Duncan & Kartesz, Long & Lakela, MacRoberts, Small (1913), or Radford *et al.*, but is included in Batson, Small (1933), and Wunderlin. There are herbarium specimens collected in Florida at locations beyond previously cultivated areas in Highlands County (Small & Mosier s. n., from scrub in hills about Lake Istokpoga [NY] and Small, Mosier, & Matthaus s. n., from scrub near Lakes Damon and Pythias [NY]), and other reported collections from "high pinelands and roadsides" near Fruitland Park, Lake County (*C. R. Williams s. n.*, [us]) and from Polk County (Wunderlin). For the purposes of this treatment it is thus considered naturalized.

South Africa, Zimbabwe, southern Mozambique, eastern and south-eastern Botswana, Malawi, and Lesotho (Abels; includes distribution maps).

Ceratotheca, distinguished by its truncate, four-horned capsules (actually two horns each splitting early during dehiscence to become four) and its fringed seeds, was described as a new genus in Endlicher's order Sesameae, which also included *Sesamum*. Although fringed seeds occur also in some species of *Sesamum*, the horned capsules continue to be a reliable diagnostic feature.

Bernhardi originally described *Ceratotheca triloba* in a new genus, *Sporledera*, even though he was aware of Endlicher's *Ceratotheca* and treated it in the same publication. Hooker reduced *Sporledera* to synonymy under *Ceratotheca* without maintaining even a separate section for it, an arrangement that has been universally followed since. Hooker's notes indicated that *C. triloba* was "closely allied to" *Sesamum orientale* but "differs from the older genus [*Sesamum*] in no important characters but the two-horned capsule, and might well be regarded as a section of it." This suggestion, which would result in the transfer of the species of *Ceratotheca* to *Sesamum*, has not generally been followed (however, cf. Baillon, 1887). More recent indications of affinity are numerous. These include the production of sterile intergeneric hybrids between species of *Ceratotheca* and *Sesamum* (Van Rheenen, 1970; Tribe); the occurrence of some fruits of *S. radiatum* Schum. & Thonn. (doubly beaked) and *C. sesamoides* (lacking horns) that are possibly transitional between *Sesamum* and *Ceratotheca* (Abels); and the postulates that *Ceratotheca* may have diverged from *Sesamum* later than some species of *Sesamum* did from each other (Abels; Ihlenfeldt & Grabow-Seidensticker) or that *Ceratotheca* may have possibly contributed to the ancestry of *Sesamum* sect. *Sesamum* in a reticulate manner (Ihlenfeldt & Grabow-Seidensticker). Evolutionary relationships between the two genera need further study.

Ceratotheca triloba has doubly fringed seeds and is distinguished from other species of *Ceratotheca* by the combination of its often trilobed leaves, corolla size (often longer than 2.5 cm), fruits obovate in outline, and fruit horns nearly horizontal (Abels). It has been reported to have a strong, unpleasant odor like that of *Hyoscyamus niger* L. (Stapf, 1906).

The other species of *Ceratotheca* are *C. sesamoides*, $2n = 32$, (fruits strongly compressed laterally [and in this feature transitional to *Sesamothamnus* Welw., which is possibly basal in the family], seeds with a single fringe all the way around, horns oblique or absent) from sub-Saharan and eastern Africa; *C. integribracteata* Engler (leaves ovate to elliptical, seeds with a single apical and a double basal fringe), from Angola and adjacent countries; *C. saxicola* E. A. Bruce (leaves and fruits smaller than those in the other species, seeds with a single fringe), from a small area in southern Africa at the edge of the ranges of *C. sesamoides* and *C. triloba*; and *C. reniformis* Abels (leaves usually

kidney shaped, seeds with two fringes, fruits broader near the base than at the apex, and fruit horns often erect), from Angola and adjacent countries (Abels; Bruce *et al.*).

Abels's monograph of *Ceratotheca* and *Dicerocaryum* Bojer is the latest and most complete treatment of the genus. On the basis of comparative seed morphology, supported by fruit characters (horn length), Abels postulated that the ancestor of *C. sesamoides* was the first to separate from the ancestors of the other species in the genus. Among the other four species, the ancestor of *C. integribracteata*/*C. saricola* is believed to have separated from that of *C. triloba*/*C. reniformis* next, followed later by separation of *C. integribracteata* from *C. saricola* and *C. triloba* from *C. reniformis*. This hypothesis is reinforced by the geographic distributions of the species, which are explainable by climatic fluctuations causing alternating advances and retreats of forest and savanna habitats. The present wide geographical separations of *C. integribracteata* from *C. saricola* and *C. triloba* from *C. reniformis* may have resulted from relatively recent fragmentation of previously continuous suitable habitats. Other characters, such as habit, seed number, fruit length, and leaf shape, do not fully support the hypothetical arrangement (Abels, pp. 233–235). The genus has not been subdivided.

Ceratotheca triloba tends to prefer relatively dry, warm areas in well-drained soils both in the United States and its natural range. Flowering in naturalized representatives in our area is from June through August. Flowers of *Ceratotheca*, like those of *Sesamum*, are structurally bee-pollinated (melittophilous; Vogel), but confirmation by field observations is needed.

Pollen of *Ceratotheca* is of the Sesameae type (an amorphous middle layer of exine present between the sexine and the nexine) (Straka). The pollen of the species of *Ceratotheca* differs within this type. Pollen of *C. sesamoides*, probably the most primitive member of the genus, is (6) 7–8 colpate and is of the *Sesamum* subtype (the sexine approximately as thick at the margins of the mesocolpi as between them). Pollen of *C. integribracteata* is (8) 9 (10) colpate and is of the *Dicerocaryum* subtype (the sexine tenuimarginate, i.e., thinner at the margins of the mesocolpi than between them). Pollen of *C. triloba* is (8) 9 (10) colpate and is transitional between the two subtypes. This reinforces the closeness of these three genera, despite their distinctive fruits, as reflected in Ihlenfeldt & Grabow-Seidensticker's classification.

The staminode representing a rudimentary fifth stamen in *Sesamum* and other genera of Pedaliaceae is usually reported to be absent in *Ceratotheca*. Observations during preparation of this treatment confirmed this. However, field observations of large numbers of flowers would help to confirm that this is always true. Bernhardt explicitly downgraded this character, partly because he had little material to work with, and it has occasionally been reported in passing that the staminode is present (e.g., Small, 1933).

As in *Sesamum*, there are both micropylar and chalazal endosperm haustoria in *Ceratotheca* (Schnarf).

Growth rings occur in stems over a year old in *Ceratotheca triloba*; latewood vessels are narrower than earlier ones. Vessels are mostly in groups. Perforation plates are simple. Lateral wall pits are mostly oval, with narrowly oval apertures in vessel-to-vessel contacts. Multiseriate rays are much more frequent than uniseriate ones. In both types, upright, square, and procumbent cells are common. These features, which place *Ceratotheca* close to *Sesamum*, are also typical of Pedaliaceae and the Scrophulariales (Carlquist).

Little is known of chemistry in *Ceratotheca*. However, leaves of *C. triloba* have been tested for saponins, leucoanthocyanins, cyanogenesis, and tannins, with a negative result for the first three and a doubtful positive one for the fourth (Gibbs). Seed oil of *C. sesamoides* does not contain sesamolin (Hegnauer).

Ceratotheca sesamoides is cultivated to some extent in Africa as an oilseed crop. Its seeds contain smaller percentages of oil than those of sesame. Both its leaves and seeds are also eaten there. Our *C. triloba* is cultivated as a garden ornamental and conservatory plant (Bailey) and has also been reported in cultivation in the United Kingdom (Hooker) and India (Cooke).

REFERENCES:

Under family references see BAILEY; BAILEY *et al.*; BATSON; BOLKHOVSKIKH *et al.*; BRUCE, 1933a, b; DE CANDOLLE; CARLQUIST; OLEWELL; COOKE; DUNCAN & KARTESCH; ERDMAN; GIBBS; HEGNAUER; HEINE; HUTCHINSON; IHLENFELDT, 1965, 1967a, b; LONG & LAKELA; MACROBERTS; MELCHIOR; METCALFE & CHALK; MONOD; PURSEGLOVE; RADFORD *et al.*; ROTH; SCHNARF; SMALL, 1913, 1933; SOLEREDER; STAFF, 1895, 1906; STOPP; STRAKA; STRAKA & IHLENFELDT; UPHOF; VOGEL; and WUNDERLIN.

ABELS, J. Die Gattungen *Ceratotheca* Endl. und *Dicerocaryum* Boj. (Monographien der afrikanischen Pedaliaceae III-IV). Mem. Soc. Broteriana 25: 1-358. 1975. [The most thorough existing treatment of *Ceratotheca*, including morphology, morphometrics, anatomy, development, geography, ecology, distribution, associated plants, taxonomic history and revision, evolutionary hypotheses, and an extensive bibliography.]

BAILLON, H. Notes sur les Pédaliniées. Bull. Mens. Soc. Linn. Paris 84: 665-671. 1887. [*Ceratotheca* treated as a section of *Sesamum*; gynoeical characters emphasized, Martyniaceae thus separated.]

BALONIA-IWANOWSKA, G. Contribution à l'étude du sac embryonnaire chez certains gamépétales. Flora 86: 47-71. 1899. [*Ceratotheca biloba* (sic), 60, 70; embryo sac illustrated, pl. 9/10, fig. 44.]

BERNHARDI, J. J. Ueber die Gattungen der Sesameae. Linnaea 16: 29-42. 1842. [Incl. original description of *Ceratotheca triloba*, but as part of a new genus *Sporledera* (= *Ceratotheca* in part); other species of *Ceratotheca* retained in *Ceratotheca*; *Sesamum* as presently understood divided into three genera.]

BRUCE, E. A., A. BRUECKNER, R. A. DYER, P. KIES, & J. C. VERDOORN. Newly described species. Bothalia 6: 213-248. 1951. [*Ceratotheca saccicola* E. A. Bruce, a species of rock crevices that lacks glandular pubescence, described and distinguished from *C. triloba*.]

- ENDLICHER, S. *Ceratotheca*, eine neue Pflanzengattung aus der Ordnung der Sesameen. *Linnaea* **7**: 1-42. 1832. [Original description of *Ceratotheca*.]
- HOOKE, J. D. *Ceratotheca triloba*. *Bot. Mag.* **114**: pl. 6974. [4 pp. text.] 1888. [Valid, effective publication of the combination (see ABELS); compared with *Sesamum*.]
- IHLENFELDT, H.-D. In: E. LAUBERT, ed., *Fl. Zambesiaca* **8**(3). 118 pp. London. 1988. [Pedaliaceae, 86-114; *Ceratotheca triloba* and other species illustrated; keys and descriptions.]
- RHEENEN, H. A. VAN. Intergeneric hybridization between *Ceratotheca sesamoides* Endl. and *Sesamum indicum* L. *Nigerian Jour. Sci.* **4**: 251-254. 1971 [1970]. [Hybrid sterile.]
- WATSON, W. *Ceratotheca triloba*. *Gard. Chron.* II. **3**: 492, 493. 1887.*

THE PIPERACEAE IN THE SOUTHEASTERN UNITED STATES¹

ALLAN J. BORNSTEIN²

PIPERACEAE Agardh, Aphor. Bot. 201. 1825, nom. cons.
(PEPPER FAMILY)

Perennial or rarely annual, aromatic herbs [shrubs, small trees, or rarely climbers], erect or repent, terrestrial or epiphytic, commonly with succulent stems and leaves, generally with spherical, ethereal oil cells embedded in the parenchymatous tissue and often with solitary or clustered crystals of calcium oxalate in parenchyma cells, vegetatively glabrous or variously with simple, multicellular hairs and/or bicellular, glandular hairs. Stems with scattered vascular bundles as in monocotyledons, but the bundles open, not closed [or arranged in 1 or 2 distinct rings, the outer of which often becomes continuous by cambial growth]; prophylls absent [present, solitary, and lateral]. Leaves

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8717333 (Carroll E. Wood, Jr., principal investigator), under which this research was conducted, and BSR-8716834 (Norton G. Miller, principal investigator). This account, the 139th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. The references that I have not verified are marked with an asterisk.

I am grateful to Carroll Wood for his support and patience during the preparation of this paper, and for his critical review of the manuscript. Thanks are offered to the curators at A, DUKE, FLAS, FSCL, FSU, FTG, GA, GH, LAF, LSU, MO, NCU, NLU, NY, SEL, UNA, USF, and VDB, for allowing me to examine specimens, either in person or on loan.

The illustration of *Peperomia* was drawn by Arnold D. Clapman (except for item b, which was drawn by Dorothy H. Marsh) under the direction of George K. Brizicky and Wood from dissections made by Wood. Drawings were made from living plants collected by Frank C. Craighead, Olga Lakela, and Wood, and cultivated at the Arnold Arboretum (except for item l, drawn from preserved material).

²Department of Biology, Southeast Missouri State University, Cape Girardeau, Missouri 63701.

©President and Fellows of Harvard College, 1991.

Journal of the Arnold Arboretum, Supplementary Series **1**: 349–366. 1991.

alternate, opposite, whorled, or basal, sessile or petiolate, the petiole often sheathing or vaginate; blades simple, entire [rarely lobed only at the base], penninerved, plinerved, or palmatinerved. Inflorescences spicate [rarely racemose], axillary, terminal, or leaf-opposed, solitary or arranged in compound structures; spikes pedunculate, the rachis often thickened, glabrous [to densely pubescent]. Flowers small, perfect [imperfect], appearing actinomorphic but developmentally zygomorphic, each subtended by a single, peltate [subpeltate or lateral], glabrous or rarely puberulent [fimbriate to densely pubescent] bract. Perianth absent. Stamens 2 [1 or 4 to 6, rarely more numerous], hypogynous or borne at the base [rarely to the middle] of the gynoecium, filaments usually shorter than the gynoecium, anthers bisporangiate and monotheous at anthesis [tetrasporangiate and ditheous], dehiscing laterally by longitudinal slits, or appearing apical due to an expanded connective; pollen inaperturate [monosulcate], binucleate. Gynoecium unicarpellate [3- or 4-carpellate], the ovary unilocular with a solitary, basal, orthotropous, unitegmie [bitegmie] ovule; style present or absent, single; stigma 1 [to 4, rarely more]. Fruits drupaceous, fleshy or dry; seeds small, with little endosperm but abundant perisperm; embryo tiny, scarcely differentiated. (Including *Peperomiaceae* (Miq.) Wettst.)
 TYPE GENUS: *Piper* L.

A large, pantropic family of two to perhaps ten genera and a very uncertain number of species, with conservative estimates in the neighborhood of 2000. By far the largest genera are *Peperomia* Ruiz & Pavón and *Piper*, into either of which nearly all taxa have been placed at one time or another. The major centers of diversity for the family are northern South America and Central America in the New World, and Malaysia in the Old World (Yuncker, 1958; Steyermark). Within the southeastern United States, only about seven species of *Peperomia* are either indigenous or have become naturalized.³

Members of the *Piperaceae* are roughly characterized as aromatic herbs or shrubs with bracteate spikes bearing numerous, perfect or imperfect flowers lacking a perianth, and with each unilocular ovary containing a single, orthotropous ovule that upon fertilization develops into a small drupe with a perispermous seed.

The question of circumscription is a major problem in the *Piperaceae sensu lato*. Several authors (e.g., Smith; Chant; Jose & Sharma) have recognized *Peperomia* and its relatives as a distinct family, serving to emphasize significant differences in habit, anatomy, anther and pollen morphology, carpel and stigma number, ovule morphology and chromosome number (see TABLE below for a comparison of these and

³Although there is no clear-cut evidence that any species of *Piper sensu stricto* or *Lepianthes* Raf. (*Pothomorphe* Miq.) have become naturalized, collections of *Piper aduncum* L., *Piper auritum* Kunth, and *Lepianthes umbellata* (L.) Raf. from apparently "wild" localities in southern Florida suggest that these species may become firmly established in the future. In the event that this does occur, the following key will allow for their identification. →

TABLE. Comparison of *Peperomia* and *Piper* with respect to various morphological features.

	<i>Peperomia</i>	<i>Piper</i>
Habit	herbaceous, often epiphytic	woody, terrestrial
Vascular system	bundles scattered (monocotyledon-like)	often in two rings (duplex)
Leaves	alternate, opposite, or whorled	alternate
Bracts	peltate; glabrous	peltate, subpeltate or laterally attached; common- ly hairy to some degree
Stamens	2	1-10 (mostly 2-6)
Anthers	bisporangiate	tetrasporangiate
Pollen	commonly inaperturate	monosulcate
Ovary	unicarpellate	tricarpetate
Stigmas	1	2-6 (commonly 3 or 4)
Ovule	unitegmic	bitegmic
Megagametophyte	<i>Peperomia</i> -type (16 nuclei)	<i>Fritillaria</i> -type (8 nuclei)
Endosperm type	cellular	nuclear
Chromosomes	$x = 11$	$x = 13$

other features in *Peperomia* and *Piper*). However, most students of the Piperales have chosen to emphasize the similarities in overall morphology, recognizing the major distinguishing features at the subfamilial (Thorne; Takhtajan) or tribal (Van Tieghem; Huber) level.

Within *Piper sensu lato*, the problem of circumscription is especially pronounced. Beginning primarily with Kunth and Miquel, several generic segregates from *Piper* were established on the basis of inflorescence type (spike vs. raceme), sexuality (monoecious vs. dioecious), style and bract morphology, stamen and stigma number, and to a lesser degree, leaf and fruit morphology. All of these segregate genera were

-
- A. Plants herbaceous, lacking swollen nodes, often succulent; leaves alternate, opposite, or whorled; gynoeceum with solitary stigma; floral bracts glabrous, often gland dotted *Peperomia*.
- A. Plants woody shrubs, small trees, or subshrubs with swollen nodes, never succulent; leaves always alternate; gynoeceum with 3 stigmas; floral bracts with fringe of whitish hairs.
- B. Inflorescences leaf-opposed, borne individually at a node; stamens 3 or more per flower; leaf blades with a distinctly unequal base.
- C. Leaf blades scabrous above, less than 9 cm broad, with glabrous margin; petioles slightly vaginate only at base, lacking conspicuous adaxial margin, shorter than inflorescence peduncle; plants lacking sarsaparilla-like odor when crushed; spikes curved in flower *Piper aduncum*.
- C. Leaf blades smooth above, greater than 12 cm broad, with densely ciliate margin; petioles deeply vaginate with thin, adaxial, persistent margin that sheaths the stem, equal to or longer than inflorescence peduncle; plants with sarsaparilla-like odor when crushed; spikes straight in flower *Piper auritum*.
- B. Inflorescences axillary spikes borne in an umbellate cluster; stamens 2 per flower; leaf blades with equal, cordate base *Lepianthes umbellata*.

later submerged in synonymy or recognized at the sectional level by De Candolle. A few of these "genera" were resurrected by subsequent workers, most notably Trelease and/or Yuncker, and additional ones created (*Sarcorhachis* Trel., *Arctotonia* Trel., *Trianaeopiper* Trel.). Recent floristic treatments of the Piperaceae recognize the most obvious segregate taxa, while using *Piper* and *Peperomia* as so-called "garbage-can" taxa. The situation is not likely to be resolved in the near future, but the most recent revisions in *Piper* (Callejas; Bornstein; Tebbs) have begun to address this problem, with the suggestion that all segregate taxa be recognized at the level of subgenus or section.

The systematic affinities of the Piperaceae are also somewhat in dispute. Whereas there is little debate that the family is most closely related to the Saururaceae, there is much less agreement as to its closeness to the Chloranthaceae, a family that has often been included in the Piperales (cf., Eames; Hutchinson; Gibbs; Burger, 1978, 1982; Xi; Cronquist, 1981, 1988; Goldberg), but which has been placed with equal frequency elsewhere in the Magnoliidae *sensu* Cronquist and Takhtajan (e.g., Laurales by Takhtajan and Metcalfe; Magnoliales by Dahlgren; Annonales, suborder Laurinae by Thorne). A similar, but less frequent, disagreement has occurred concerning the Lactoridaceae (placed in Piperales by Burger, Goldberg, and Melchior; elsewhere in the Magnoliidae by Cronquist, Dahlgren, Takhtajan, and Thorne).

Considering the large size of the family, relatively few (a dozen or so) species have been appropriately analyzed chemically. However, from these species a wide variety of compounds have been reported, including aromatic terpenoids (mono- and sesquiterpenes), flavonoids (flavones and C-glycoflavones), alkaloidal amines, pyridine or aporphine alkaloids, phenols, phenolic esters, and ethers. Whether this information is taxonomically useful remains to be seen.

The Piperaceae are not especially important economically other than *Piper nigrum* L., source of black and white pepper, which is certainly one of the oldest and most important of the world's spices (see Brown & Reader; Gentry; Guenther; Menon; Purseglove; Purseglove *et al.*; and Yuncker, 1958). Other species of *Piper* are important locally for medicinal or food purposes (e.g., *Piper angustifolium* Ruiz & Pavón, matico, used as a stimulant and hemostatic; *Piper Cubeba* L., cubeb, used to relieve bronchitis, asthmatic conditions, throat irritations, and gonorrheal discharges; *Piper longum* L., long-pepper, used in native curries), or in some cases have become a part of religious or ritualistic ceremonies (e.g., *Piper methysticum* Forst. f., source of the non-alcoholic beverage known as kava, which is used extensively in the Polynesian islands for its mild narcotic effects; *Piper Belle* L., the betel pepper or betel vine, a leaf of which is wrapped around slices of betel nut (*Areca Catechu* L.), smeared with lime and used as a masticatory much like chewing tobacco, presumably acting as a stimulant). Species of *Peperomia* are important as ornamentals, often grown as house plants for their attractive foliage (see Bailey *et al.*).

REFERENCES:

- BAI, G. V. S., & D. SUBRAMANIAN. Cytotaxonomical studies of South Indian Piperaceae. *Cytologia* 50: 583–592. 1985. [Incl. observations on 21 species, including *Peperomia magnoliifolia*, *P. obtusifolia*, and *P. pellucida*.]
- BAILLON, H. E. Piperaceae. *Hist. Pl.* 3: 465–496. 1872. [Incl. Saurureae, Pipereae, Chloranthaeae, and Ceratophylleae in Piperaceae.]
- BAILEY, L. H., E. Z. BAILEY, & BAILEY HORTORIUM STAFF. *Hortus* third. xiv + 1290 pp. New York and London. 1976. [*Peperomia*, 843–845; *Piper*, 877, 878.]
- BENSON, L. Plant classification. xiv + 688 pp. Boston. 1957. [Piperales, 189, 190; includes Saururaceae, Piperaceae, Chloranthaceae; mentions *Peperomia* occurring in Florida.]
- BENTHAM, G. Piperaceae. In: G. BENTHAM & J. D. HOOKER, *Gen. Pl.* 3: 125–133. 1880. [Two tribes recognized on the basis of carpel and ovule number: Saurureae (including *Lactoris*) and Pipereae.]
- BESSEY, C. E. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109–164. 1915. [Piperaceae, 129; placed in Ranales with Saururaceae and Chloranthaceae.]
- BLANC, P., & K. ANDRAOS. Remarques sur la dynamique de croissance dans le genre *Piper* L. (Piperaceae) et les genres affines. *Bull. Mus. Hist. Nat. Paris B. Adansonia* 3: 259–282. 1983. [Discusses growth habit and variations in *Piper* and relatives.]
- BOIVIN, B. Les familles de trachéophytes. *Bull. Soc. Bot. France* 103: 490–505. 1956. [Piperales includes Piperaceae, Saururaceae, Chloranthaceae, Lacistemataceae.]
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. A. A. FEDOROV, ed. (Russian and English pref. aces.) 926 pp. Leningrad. 1969. [Piperaceae, 486, 487.]
- BORNSTEIN, A. J. Taxonomic studies in the Piperaceae. I. The pedicellate pipers of Mexico and Central America (*Piper* subg. *Arctottonia*). *Jour. Arnold Arb.* 70: 1–55. 1989. [Pertinent information on taxonomic history and classification of *Piper*.]
- BREWBAKER, J. L. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. *Am. Jour. Bot.* 54: 1069–1083. 1967. [Piperaceae, 1080; *Peperomia* and *Piper* with binucleate pollen.]
- BROWN, E., & D. E. READER. Pepper; cultivation and marketing of the world's leading spice. *Coffee & Tea Industr.* 77: 105–106. 1954.
- BURGER, W. C. Flora Costaricensis: Family 41. Piperaceae. *Fieldiana Bot.* 35: 5–227. 1971.
- . Evolutionary trends in the Central American species of *Piper* (Piperaceae). *Brittonia* 24: 356–362. 1972. [Habit, prophyll morphology, inflorescence morphology, and anther dehiscence discussed from an evolutionary perspective.]
- . The Piperales and the Monocots: alternate hypothesis for the origin of monocotyledonous flowers. *Bot. Rev.* 43: 345–393. 1978.
- . Chloranthaceae are related to the Piperales, an ancient dicotyledonous alliance (Abstr.). *Bot. Soc. Am. Misc. Publ.* 162: 87. 1982. [Argues that the Piperales, including Chloranthaceae and Lactoridaceae, are a more primitive assemblage than the Magnoliales/Laurales.]
- CALLEJAS, R. Taxonomic revision of *Piper* subgenus *Ottonia* (Piperaceae). Unpubl. Ph.D. dissertation, City University of New York. 1986. [Includes important preliminary cladistic analysis of the genus.]
- CANDOLLE, C. DE. Piperaceae. *DC. Prodr. Syst. Nat. Veg.* 16(1): 235–471. 1869.
- CHANT, S. R. Peperomiaceae. P. 40 in V. H. HEYWOOD, ed., *Flowering plants of the world*. New York. 1978. [*Manekia*, *Piperanthera*, *Verhuellia*, and *Peperomia*.]
- CHAPMAN, A. W. Flora of the southern United States. ed. 3. xxxix + 655 pp. New York, Cincinnati, Chicago. 1897. [Piperaceae, 418, 419; includes *Saururus* and *Peperomia*.]

- CORNER, E. J. H. The seeds of dicotyledons. Vol. 1. x + 311 pp. Cambridge, England. 1976. [Piperaceae, 43, 44, 217, 218; considers Chloranthaceae to be clearly distinct from Piperaceae/Saururaceae on the basis of seed morphology.]
- CRONQUIST, A. An integrated system of classification of flowering plants. xviii + 1262 pp. New York. 1981. [Piperaceae, 86-89; Piperales includes Piperaceae, Saururaceae, and Chloranthaceae.]
- . The evolution and classification of flowering plants. viii + 555 pp. New York. 1988. [Piperales, 280-283; suggests origin of order from Magnoliales rather than Laurales.]
- DAHLGREN, R. M. T. A revised system of classification of the angiosperms. Bot. Jour. Linn. Soc. 80: 91-124. 1980. [Piperales (Saururaceae and Piperaceae) included with Nymphaeales in the Nymphaeiflorae, primarily on the basis of similar seeds (perispermous) and the presence of S-type sieve-tube plastids and sulcate pollen; see also Nordic Jour. Bot. 3: 119-149. 1983.]
- DASGUPTA, A., & P. C. DATTA. Cytotaxonomy of Piperaceae. Cytologia 41: 697-706. 1976. [Suggest, on the basis of chromosome number, that *Peperomia* is more primitive than *Piper*.]
- DATTA, P. C., & A. DASGUPTA. Comparison of vegetative anatomy of Piperales: I. Juvenile xylem of twigs. Acta Biol. Acad. Sci. Hung. 28: 81-96. 1977a.
- & ———. Comparison of vegetative anatomy of Piperales: II. Leaf. *Ibid.* 97-110. 1977b.
- & ———. Comparison of vegetative anatomy of Piperales: III. Vascular supplies to leaves. Acta Bot. Indica 7: 39-46. 1979.
- DAVIS, G. L. Systematic embryology of the angiosperms. viii + 528 pp. New York, London, and Sydney. 1966. [Piperaceae, 210, 211.]
- EAMES, A. J. Morphology of the angiosperms. *Frontisp.* + xiii + 518 pp. New York, Toronto, and London. 1961. [Incl. Chloranthaceae in Piperales.]
- ENGLER, A. Piperaceae. In: A. ENGLER & K. PRANTL, Nat. Pflanzenfam. III. 1: 3-11. 1887.
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. *Frontisp.* + xii + 539 pp. Uppsala. 1966. [Piperaceae, 321, 322.]
- GENTRY, H. S. Introducing black pepper into America. Econ. Bot. 9: 256-268. 1955. [Account of the numerous varieties of this important spice, with notes concerning cultivation and harvesting.]
- GISBS, R. D. Chemotaxonomy of flowering plants. 4 vols. xx + 2372 pp. Montreal and London. 1974. [Piperales, Vol. 3, 1530-1539; Piperaceae, 1532, 1533; summary of chemistry of Saururaceae, Chloranthaceae, Piperaceae, and Lactoridaceae, with discussion and conclusion that first three families belong together.]
- GOLDBERG, A. Classification, evolution, and phylogeny of the families of dicotyledons. Smithsonian Contr. Bot. 58: 1-314. 1986. [Piperaceae, 6, 67, 68; placed in Piperales with Saururaceae, Chloranthaceae, and Lactoridaceae.]
- GORNALL, R. J., B. A. BOHM, & R. DAHLGREN. The distribution of flavonoids in the angiosperms. Bot. Not. 132: 1-30. 1979. [Flavones and C-glycoflavones characterize the Piperaceae; a possible supportive link to the monocots?]
- GROFF, G. W. Piperales of Kwangtung, China. Lingnan Sci. Jour. 11: 81-100. 1932. [Piperaceae, 86-94; basic reference with worthwhile notes concerning the economic value of various species of *Piper*.]
- GUENTHER, E. S. The essential oils. Vol. V. xvii + 507 pp. Toronto, New York, London. 1952. [Piperaceae, 135-161; detailed account of pepper oil (*Piper nigrum*), cubeb oil (*Piper Cubeba*), and other minor species.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Vol. 5. Basel und Stuttgart. 506 pp. 1969. [Piperaceae, 311-324.]
- HUBER, H. Piperaceae. Pp. 272-300 in M. D. DASSANAYAKE & F. R. FOSBERG, eds., A revised handbook to the Flora of Ceylon. Vol. VI. New Delhi. 1987.

[Useful introductory comments; divides the family into two tribes, *Pipereae* and *Peperomieae*.]

- HUTCHINSON, J. The families of flowering plants. ed. 3. xviii + 968 pp. Oxford. 1973. [*Piperales*, 513-519; includes *Saururaceae*, *Piperaceae*, and *Chloranthaceae*.]
- JOHNSON, D. S. On the development of certain *Piperaceae*. *Bot. Gaz.* 34: 321-340. 1902. [*Piper*, *Heckeria* (= *Lepianthes*), and *Peperomia* examined with respect to various features of the ovules, seeds, and fruits; considers *Peperomia* to be the most evolutionarily advanced.]
- JOSE, J., & A. K. SHARMA. Structure and behavior of chromosomes in *Piper* and *Peperomia* (family *Piperaceae*). *Cytologia* 50: 301-310. 1985. [*Piper* primarily with $x = 13$ and *Peperomia* with $x = 11$; consider that two families should be recognized (*Piperaceae* and *Peperomiaceae*) and that *Peperomia* is primitive.]
- JUSSIEU, A. L. DE. *Genera plantarum secundum ordines naturales disposita*. lxxii + 498 pp. Paris. 1791. [*Piper*, 405, 406; placed in "Genera Urticis affinis."]
- KONOSHIMA, M., & T. MIYAGAWA. Pharmacognostical studies on the piperaceous plants: 1. Studies on the crude drugs of stems: 1. On *Piper* section *Chavica*. *Syoyakugaku Zasshi* 30: 138-154. 1977a.*
- & ———. Pharmacognostical studies on the piperaceous plants: 2. Studies on the crude drugs of stems: 2. On *Piper* sections *Eupiper* and *Cubeba*, and *Peperomia*. *Ibid.* 30: 155-163. 1977b.*
- KUNTH, K. S. Bemerkungen über die Familie des *Piperaceen*. *Linnaea* 13: 561-726. 1839. [Recognizes six generic segregates from *Piper sensu lato*.]
- KUPICHA, F. K. *Piperaceae*. P. 38 in V. H. HEYWOOD, ed., *Flowering plants of the world*. New York. 1978. [*Piper* (ca. 2000 spp.) or possibly several small segregate genera (e.g., *Ottonia*, *Pothomorphe*, and *Sarcorhachis*).]
- LE MAOUT, E., & J. DECAISNE. *Traité général de botanique descriptive et analytique*. viii + 746 pp. London. 1873. [English translation.] [*Piperaceae*, 728-731.]
- LINDLEY, J. *The vegetable kingdom*. ed. 3. lxxviii + 908 pp. London. 1853. [*Piperaceae*, 515-518; included with *Saururaceae* and *Chloranthaceae* in *Piperales*.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. 2 vols. New York. 1892. [*Piperaceae*, 2: 446-448.]
- MAHESHWARI, P. The angiosperm embryo sac. *Bot. Rev.* 14: 1-56. 1948. [*Peperomia*, 15-17; *Piper*, 21.]
- MARTIN, F. W., & L. E. GREGORY. Mode of pollination and factors affecting fruit set in *Piper nigrum* L. in Puerto Rico. *Crop. Sci.* 2: 295-299. 1962. [Suggest that wind pollination is not very effective in cultivated peppers; self-fertilization, aided by water distribution of the pollen, is common.]
- MATHEW, P. M. Studies on *Piperaceae*. *Jour. Indian Bot. Soc.* 37: 155-171. 1958. [Chromosome number reports; suggests $x = 13$ for *Piper* and *Heckeria* (= *Lepianthes*), $x = 11$ for *Peperomia*.]
- MELCHIOR, H. *Piperales*. Pp. 147-151 in H. MELCHIOR, A. Engler's *Syllabus der Pflanzenfamilien*. ed. 12. Vol. 2. Berlin. 1964. [Incl. *Piperaceae*, *Saururaceae*, *Chloranthaceae*, and *Lactoridaceae*.]
- MENON, K. K. The survey of *pollu* and root diseases of pepper. *Indian Jour. Agr. Sci.* 19: 89-136. 1949. [Important reference concerning cultivated *Piper nigrum*; suggests that pollination is aided by monsoon rains.]
- METCALFE, C. R. *Anat. Dicot.* ed. 2. 3: 143-145, 151, 156. 1987. [Comments on relationship of *Piperaceae* (*Piperales*) with *Chloranthaceae*, *Lactoridaceae*, and *Lauraceae*.]
- & L. CHALK. *Piperaceae*. *Anat. Dicot.* 2: 1120-1127. 1950.
- MIQUEL, F. A. G. *Systema Piperacearum*. Rotterdam. 1843-44. [Important monographic work.]

- MIYOSHI, N., & H. KATO. Pollen morphology by means of scanning electron microscope: 5. Angiospermae. (Piperales, Podostemonales). Jap. Jour. Palynol. **28**: 7-11. 1982.*
- NIKITICHEVA, Z. I. Embryological features of some Piperales. Acta Soc. Bot. Polon. **50**: 329-332. 1981. [Discusses basic embryological aspects of Piperaceae and Saururaceae from a comparative perspective.]
- OKADA, H. Karyomorphology and relationships in some genera of Saururaceae and Piperaceae. Bot. Mag. Tokyo **99**: 289-299. 1986. [Suggests a basic chromosome number of $x = 11$ for the Piperaceae/Saururaceae; two major types of karyomorphology recognized, with species of *Peperomia* distinct from the other genera studied.]
- PANT, D. D., & R. BANERJI. Structure and ontogeny of stomata in some Piperaceae. Jour. Linn. Soc. Bot. **59**: 223-228. 1965. [A variety of stomatal patterns, including amphicyclid, anisocytic, anomocytic, and tetracytic, observed in the few taxa examined.]
- PURSEGLOVE, J. W. Tropical crops. Dicotyledons 2. viii + 333-719 pp. London. 1974. [Piperaceae, 436-450; specifically covers *Piper Betle* and *Piper nigrum*.]
- , E. G. BROWN, C. L. GREEN, & S. R. J. ROBBINS. Spices. Vol. 1. New York. 1981. [Pepper, 10-99; wealth of information concerning all aspects of this commercially important crop.]
- RAVEN, P. H., & D. J. AXELROD. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. **61**: 539-673. 1974. [Suggest Laurasian origin for Piperaceae, "perhaps reaching South America via Africa," 562.]
- RENDLE, A. B. The classification of flowering plants. Vol. 2. Dicotyledons. ed. 2. xix + 640 pp. Cambridge, England. 1952. [Piperales, 88-93; includes Piperaceae, Saururaceae, and Chloranthaceae.]
- ROUSSEAU, D. Contribution à l'anatomie comparée des Pipéracées. Mém. Acad. Roy. Belg. II. **9**: 1-45. 1927. [Detailed account of the stem anatomy of selected species in the family (includes Saururaceae).]
- SAMUEL, R. Chromosome numbers in *Piper*. Kew Bull. **42**: 465-470. 1986. [New counts and table of previous reports; $x = 13$.]
- SARALEGUI BOZA, H. Algunas consideraciones generales sobre el Orden Piperales en Cuba. Wiss. Zeitschr. Friedrich-Schiller Univ. Jena. Math.-Naturw. Beitr. Phytotax. **28**: 639-642. 1979.*
- SCHLEIFFER, H., ed. Narcotic plants of the Old World used in rituals and everyday life: an anthology of texts from ancient times to the present. 193 pp. New York. 1979. [Piperaceae, 125-136; texts concerning *Piper methysticum* (ritual use).]
- SCHULTES, R. E. De plantis toxicariis e munde novo tropicale commentationes: 12. Notes on biodynamic piperaceous plants. Rhodora **77**: 165-170. 1975. [Ethnopharmacology of New World Piperaceae.]
- SEMPLE, K. S. Pollination in Piperaceae. Ann. Missouri Bot. Gard. **61**: 868-871. 1974. [First documented evidence of insect pollination in neotropical pipers.]
- SENGUPTA, S., & A. B. RAY. The chemistry of *Piper* species: A review. Fitoterapia **58**: 147-166. 1987. [Detailed account of the numerous compounds isolated from different species of *Piper*.]
- SMITH, A. C. Flora Vitiensis Noya. A new flora of Fiji. Vol. 2. Honolulu, Hawaii. 1981. [Piperales, 56-97; includes Piperaceae and Peperoniaceae; information concerning economic uses of Old World species.]
- STEINMETZ, E. F. Kava-kava, famous drug plant of the South Sea islands. 36 pp. New York and San Francisco. 1973. [Popular account of the botany, chemistry, history, cultivation, preparation, and use of this Polynesian beverage.]
- STEYENMARK, J. A. Piperaceae. In: Flora of Venezuela. Vol. 2, pt. 2. 619 pp. Caracas. 1984. [*Peperomia*, *Piper*, *Polthomorphis* (2 spp.), *Sarcorhachis* (1 sp.).]

- TAKHTAJAN, A. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46**: 225-359. 1980. [Piperales, 260; includes Piperaceae and Saururaceae; origin nearest to Laurales; probable common origin with Chloranthaceae and Lactoridaceae.]
- TEBBS, M. C. Revision of *Piper* (Piperaceae) in the New World. 1. Review of characters and taxonomy of *Piper* section *Macrostachys*. Bull. Brit. Mus. Nat. Hist. Bot. **19**: 117-158. 1989. [Most importantly discusses classification of *Piper* and compares with other suggested genera of Piperaceae.]
- THORNE, R. F. A phylogenetic classification of the Angiospermae. Evol. Biol. **9**: 35-106. 1976. [Piperaceae in order Annonales, suborder Piperineae with the Saururaceae; see also Nordic Jour. Bot. **3**: 85-117. 1983.]
- TIEGHEM, P. VAN. Sur les canaux à mucilage des Piperées. Ann. Sci. Nat. Bot. IX. **7**: 117-127. 1908. [Anatomical analysis of mucilage canals in stems and leaves.]
- TRELEASE, W., & T. G. YUNCKER. The Piperaceae of northern South America. 2 vols. Urbana. 1950.
- TUCKER, S. C. Inflorescence and flower development in the Piperaceae: I. *Peperomia*. Am. Jour. Bot. **67**: 686-702. 1980. [*Peperomia* flowers characterized as bilaterally symmetrical and uncarpellate.]
- . Inflorescence and flower development in the Piperaceae: III. Floral ontogeny of *Piper*. Ibid. **69**: 1389-1401. 1982. [*Piper* flowers characterized as bilaterally symmetrical and 3- or 4-carpellate.]
- VOGEL, E. F. DE. Seedlings of dicotyledons. The Netherlands. 1980. [*Piper* and *Peperomia* with *Macaranga* or *Endertia* (*Peperomia*) type seedlings.]
- WAHAL, D., & B. R. JUNCJA. Bibliography on "pan": *Piper Betle* Linn. viii + 49 pp. Lucknow, Economic Botany Information Service, National Botanical Research Institute. 1979.
- WEBERLING, F. Weitere Untersuchungen zur Morphologie des Unterblattes bei den Dikotylen. V. Piperales. Beitr. Biol. Pflanzen. **46**: 403-434. 1970. [Examination of leaf base morphology among Piperaceae, Saururaceae, Lactoridaceae, and Chloranthaceae; apparent close relationship between first three families, but not the last.]
- XI, Y.-Z. Studies of pollen morphology and its systematic position in the order Piperales. Acta Bot. Sinica **22**: 323-329. 1980. [Chloranthaceae placed in Piperales and considered most primitive family in the order. Piperales viewed as closely related to monocot/dicot ancestor.]
- YUNCKER, T. G. The Piperaceae—a family profile. Brittonia **10**: 1-7. 1958. [Important summary of the family from an historical perspective, with comments on economic value and phylogeny.]
- . A bibliography of the family Piperaceae. Candollea **19**: 97-144. 1964. [An essential reference.]

1. *Peperomia* Ruiz & Pavón, Prodrum 8. 1794.

Annual or perennial herbs, terrestrial or epiphytic, erect or repent, commonly succulent; stems with numerous, scattered vascular bundles. Leaves alternate, opposite, or whorled, simple, petiolate [or not], exstipulate; blades entire, usually succulent, commonly with glandular dots, but these often visible only on dried specimens; plants glabrous or with simple, uniseriate hairs. Inflorescences axillary, terminal, or leaf-opposed, solitary or paired at a node, or more numerous in those species with whorled leaves, the spikes simple [or compound and variously arranged], with a succulent rachis, glabrous to puberulent. Flowers

subtended by a peltate, orbicular bract, glabrous but often glandular-dotted; stamens 2 with short filaments and bisporangiate, monothealous anthers; gynoecium unicarpellate, sessile [or pedicellate], with solitary, apical or subapical, commonly fimbriate stigma, a beak developed or not; ovule solitary, unitegmic, with tetrasporic, 16-nucleate embryo sac. Fruits sessile [or pedicellate or pseudopedicellate], variously shaped from globose to subcylindrical, the surface viscid and often verrucose, rarely longitudinally striate. Base chromosome numbers 11 or 12. (Including *Micropiper* Miq.; *Rhynchophorum* (Miq.) Small.) LECTOTYPE SPECIES: *P. secunda* Ruiz & Pavón.⁴ (Pepper-like, in reference to the similarity of these plants to members of the genus *Piper*.) — WILD PEPPERS, PEPEROMIAS.

A genus variously estimated to consist of 600–1000 species. The former number is probably closer to reality, especially when one considers that previous workers often recognized “new” species on the basis of characters known to be rather variable (e.g., leaf size and shape; pubescence). *Peperomia* is principally a New World genus, best developed in the tropics from central Mexico south through Central America, the West Indies, and into South America. It is extensively distributed throughout Hawaii and the Polynesian islands, and is also represented in Malesia, portions of India, southeastern Asia, Australia, and tropical Africa. About seven species occur in the Southeast.

Within the tribe Peperomieae, Miquel recognized *Peperomia* with four subgenera, and four segregate genera. Dahlstedt subsequently divided *Peperomia* into nine subgenera and seven sections, largely on the basis of characteristics of the fruit. Trelease essentially followed Dahlstedt's views, but did raise two of his sections to subgeneric status for a total of eleven subgenera. With the exceptions of Yuncker (1974), who combined a few of Dahlstedt's subgenera, eventually recognizing five in all, and Burger (1971), who seriously questioned the development of the pseudocupule that typifies subgenus *Micropiper* (Miq.) Dahlst., Dahlstedt's treatment has been largely unchallenged. This account attempts to follow the more conservative treatment of Yuncker.

Subgenus ACROCARPIDIUM (Miq.) Dahlst. (including subg. *Pleurocarpidium* Dahlst.), easily characterized by the presence of pedicellate fruits, is very questionably represented in our area by *Peperomia emarginella* (Wiks.) C. DC. This species is recognized by its delicate

⁴Ruiz & Pavón did not designate a type in either the original generic description of *Peperomia* or in their more extensive treatment four years later (Fl. Peruv. Chil. 1: 29–33. 1798). According to Howard (1973), Britton (Fl. Bermuda 94. 1918) was the first to have chosen *Peperomia secunda* as a “type species,” and this designation is listed in the ING. Other reported lectotypes include *Peperomia scutellaeifolia* Ruiz & Pavón by Britton & Wilson (Bot. Porto Rico 5: 223. 1924) and *Peperomia pellucida* (L.) Kunth by Trelease & Yuncker; both choices must be rejected in favor of the earliest chosen type. With *Peperomia secunda* the lectotype of the genus, subgenus *Panicularia* Miq., which includes this species, becomes a synonym of the autonymic subgenus *Peperomia*.



FIGURE 1. *Peperomia*. a, *P. glabella*: leaf, $\times 1/2$. b–g, *P. humilis*: b, flowering shoot, $\times 1/2$; c, portion of inflorescence, $\times 6$; d, flower with subtending bract, showing gynoeceum and two stamens, $\times 18$; e, gynoeceum, $\times 18$; f, portion of spike with a mature fruit, showing drupe (with glandular exocarp) subtended by floral bract, $\times 12$; g, endocarp, $\times 18$. h–l, *P. obtusifolia*: h, flowering shoot, $\times 1/2$; i, flower with subtending bract, gynoeceum, and two stamens, $\times 18$; j, bract, lateral view, attachment of bract to the left, $\times 18$; k, tip of spike with partly mature fruits, three removed to show immersion of base of fruit in tissue of axis, apex of spike with undeveloped flowers shown only in outline—note small unpollinated gynoecea between developing fruits, $\times 6$; l, mature drupe, lateral view, showing hooked apex and position of stigma, $\times 12$.

appearance; epiphytic, prostrate habit; minute, ovate to orbiculate, often emarginate, alternate leaves; and slender spikes with few, distant flowers. Boufford lists this species on the basis of a single collection labeled "Alto, 7–16–1915, F. & S. 8725" sent on loan from the New York Botanical Garden. It seems much more plausible that this specimen is from elsewhere in the range of this species, which includes the West Indies, Central America, and northern South America.

Subgenus *TILDENIA* (Miq.) Dahlst. (including subg. *Ogmocarpidium* Dahlst.) is characterized by sessile, apically mammiform or stylose fruits lacking a pseudocupule and the stigma apical. The only species of this subgenus in our area is the widespread annual weed *Peperomia pellucida* (L.) Kunth, pepper-elder, rat-ear, $2n = 44$ (20, 22, 24, and 46 also recorded), native to the Neotropics, but also known from the Old World. It is readily recognized by the broadly ovate to shallowly cordate, glabrous, alternate leaves, that dry thin and translucent, and the globose-ovoid fruits with prominent longitudinal ridges. Given the weedy nature of this species, it is not surprising that this species has become naturalized in the southeastern United States. It is the only species that has been collected outside of Florida, occurring in Georgia, Alabama, and Louisiana, often around nurseries or greenhouses.

Subgenus *MICROPIPER* is not represented in the southeastern United States. Dahlstedt recognized this taxon on the basis of a so-called "pseudocupule." Burger (1971) considers this to be a non-morphological feature that represents "the differential drying of the lower part of the [viscid] fruit-surface in contact with the enclosing rachis." The presence of this feature varies on the same inflorescence and is therefore of questionable taxonomic value.

Subgenus *RHYNCHOPHORUM* (Miq.) Dahlst. consists of erect or repent plants, rooting at the lower nodes, with thick, obovate to oblong-lanceolate to cordate (then usually peltate), alternate leaves; fruits ellipsoidal or cylindrical, sessile and basally attached, with a scutelliform or rostrate apex, the stigma centrally located in the viscid tissue that forms the scutellum or rostrum. This widespread group, with numerous species located throughout the Neotropics, is represented in our area by the following three species.

Peperomia amplexicaulis (Sw.) A. Dietr., presumably endemic to Jamaica, is known from two collections (*Atwater 626* (FLAS) and *Craig-head s.n.* (FTG)), both from Dade County near Cutler and Cutler Ridge. It is readily recognized by the sessile to subsessile, oblanceolate, auriculate leaves and the ellipsoidal fruit with a short beak.

Peperomia magnoliifolia (Jacq.) A. Dietr. (*Peperomia spathulifolia* Small, *Rhynchophorum spathulifolium* (Small) Small), $2n = 22$ (24, 38), is known from Dade County (Hattie Bauer Hammock and Burden's Hammock) on the basis of several collections, all made before 1923. The natural range of this species is Mexico, the West Indies, Central America, and northern South America. It is very similar to *Peperomia obtusifolia* (L.) A. Dietr. but can be distinguished from that species by the glabrous (vs. microscopically puberulent) peduncle and the subulate, gradually hooked rostrum (vs. filiform, abruptly hooked near the apex). Burger (1971) does not consider these to be biologically significant distinctions that warrant specific status, but detailed chromosomal analysis (Jose & Sharma) appears to substantiate that these species are different. Steyermark, after considerable study of these taxa, agreed that they are separable, using bract size (5–7 mm diam. vs. 2–4 mm, respectively) as an additional criterion.

Peperomia obtusifolia (*Peperomia floridana* Small, *Rhynchochloa floridanum* (Small) Small, *Rhynchochloa obtusifolium* (L.) Small), Florida peperomia, wild pepper, $2n = 22$ (24), is a species found in extreme southern Florida, extending northward as far as Brevard County. It grows in hammocks, swamps, or mangrove regions, either as a ground-cover on fallen, rotting logs, or as an epiphyte, especially on live oak (*Quercus virginiana* Miller) or pond apple (*Annona glabra* L.). It is found naturally throughout the West Indies, the Bahamas, Mexico, and Central and South America. As previously mentioned, it is often confused with *Peperomia magnoliifolia* but can be reliably distinguished on the basis of bract size, pubescence of the peduncle, and shape of the beak (rostrum). *Peperomia obtusifolia* is a commonly cultivated species, with solid green-leaved and variegated cultivars ("varieties").

Members of subgenus SPHAEROCARPIDIUM Dahlst. are characterized by a generally erect habit with decumbent base (but some species creeping); leaves alternate, opposite, or whorled, variously shaped; fruits globose-ovoid, sub-basally attached, the apex with an oblique beak and a subapical stigma. It is a widespread neotropical group represented in our area by three species.

Peperomia alata Ruiz & Pavón, a common, widespread species in Mexico, Central and South America, and the West Indies, is known from three collections (two from Collier County, near Deep Lake, the third locality unspecified). It is readily recognized by the alternate, elliptic to oblanceolate leaves with petioles clasping the stem and decurrent in two ridges or wings, the leaf apex acuminate and usually minutely puberulent at the very tip.

Peperomia glabella (Sw.) A. Dietr., cypress peperomia, native from Guatemala to northern South America and the West Indies, is known from Collier County (Fahkahatchee Strand region) on the basis of several relatively recent (post-1960) collections. It is easily recognized by the numerous black dots (most readily visible on dried specimens) on all plant parts; the alternate, succulent, three-nerved leaves; and the curved hairs arranged in two rows on the petioles, these often extending onto the stems below the nodes.

Peperomia humilis A. Dietr. (*Piper leptostachyon* Nutt., *Peperomia leptostachya* (Nutt.) Chapman, *Peperomia cumulicola* Small, *Micropiper humilis* (Vahl) Small, *Micropiper leptostachyon* (Nutt.) Small), the most wide-ranging of the three species, occurs from Duval County in northeastern Florida to Collier, Monroe, and Dade counties in the extreme southern portion of the state. It is commonly found as a terrestrial plant on limestone rock (shell middens) or as an epiphyte on live oak, pond apple, or buttonwood (*Conocarpus erectus* L.), in either case growing in a layer of humus. It is distinctive among all the peperomias in our area because of the opposite or ternate leaf arrangement and the densely pubescent stems. It is said to occur in Florida, Hispaniola, Puerto Rico, and the Lesser Antilles, but there is some question as to whether this species is truly different from *Peperomia*

blanda (Jacq.) Kunth, which is a very widespread species occurring in Mexico, Guatemala, Jamaica(?), Trinidad, and South America as far south as Bolivia, Argentina, and southern Brazil. Dahlstedt included *P. humilis* as a synonym of *P. Langsdorffii* (Miq.) Miq. Yuncker, in turn, recognized this taxon as a variety of *P. blanda*, whereas Steyermark completely submerged it under that species. The question needs to be resolved, since the name *P. blanda* has priority over *P. humilis*.

A final species, *Peperomia simplex* Ham., pale-green peperomia, endemic to Jamaica, has been reported from southern Florida by Craighead and Long & Lakela. No herbarium material of this species has been seen from anywhere in the Southeast, but it is conceivable that it has been introduced in the past, perhaps without persisting.

Information concerning pollination biology in *Peperomia* is non-existent. Floral morphology in the genus is superficially similar to that of many anemophilous "Amentiferae" (i.e., spicate inflorescence, minute flowers with reduced perianth, one ovule/ovary), but wind pollination is traditionally considered to be rare in species of tropical environments. It is equally difficult to imagine that wind pollination would be an effective mechanism for a genus that is largely epiphytic. Without a detailed study, one can only speculate.

Similarly, dispersal of the fruits in *Peperomia* is a matter of conjecture. The sticky or mucilaginous nature of the fruits in many species is suggestive of zoochory (in fact, Huber characterizes the members of subgenera *Micropiper* and *Sphaerocarpidium* as epizoochorous; *Peperomia pellucida* is considered ballautochorous), but to my knowledge, no scientific investigations have addressed this question. Indeed, studies concerning reproductive biology are sorely needed for the entire family.

REFERENCES:

- Under family references see BAI; BAILLON; BENSON; BENTHAM; BOLKHOVSKIKH, *et al.*; BREWBAKER; BURGER (1971); DE CANDOLLE; CHANT; CHAPMAN; DASGUPTA & DATTA; DATTA & DASGUPTA (1977a, b, 1979); DAVIS; ENGLER; ERDTMAN; GIBBS; HEGNAUER; HUBER; JOHNSON; JOSE & SHARMA; KONOSHIMA & MIYAGAWA (1977b); MAHESHWARI; MATHEW; METCALFE & CHALK; MIQUEL; MIYOSHI & KATO; NIKITICHEVA; OKADA; PANT & BANERJI; ROUSSEAU; SMITH; STEYERMARK; TRELEASE & YUNCKER; TUCKER (1980); DE VOGEL; XI; and YUNCKER (1958, 1964).
- ADAMS, C. D. Flowering plants of Jamaica. 848 pp. Mona, Jamaica. 1972. [Piperaceae, 202–213; all of the species listed for our area, except *Peperomia humilis*, are keyed and described; *P. simplex* included.]
- BLANC, P., & K. ANDRAOS. Remarques sur la dynamique de croissance dans le genre *Peperomia* Ruiz & Pav. (Pipeféeae). Bull. Mus. Hist. Nat. Paris B. Adansonia **6**: 41–56. 1984. [Diversity of growth habits in *Peperomia* discussed.]
- BLOT, J. Contribution à l'étude cytologique du genre *Peperomia*. Rev. Gén. Bot. **67**: 522–535. 1960. [Incl. counts of species that occur in Florida.]
- BOUFFORD, D. E. Notes on *Peperomia* in the southeastern United States. Jour. Arnold Arb. **63**: 317–325. 1982. [Important reference concerning native and introduced species, with key, synonymy, and distributional information.]
- BROWN, W. H. The nature of the embryo-sac of *Peperomia*. Bot. Gaz. **46**: 445–460. pls. 31–33. 1908. [Describes the detailed development of the 16-nucleate

embryo-sac, for three species; concludes that the *Peperomia*-type embryo-sac is a derived condition.]

CAMPBELL, D. H. A peculiar embryo-sac in *Peperomia pellucida*. *Ann. Bot.* 13: 626. 1899. [First account of the unusual embryo-sac of *Peperomia*.]

———. The embryo-sac of *Peperomia*. *Ibid.* 15: 103–118. pl. 6. 1901. [More detailed account than his earlier paper, with comments about the evolutionary position of *Peperomia*.]

CORBETT, M. K. Virus ring spot of *Peperomia obtusifolia* and *Peperomia obtusifolia* var. *variegata*. *Proc. Florida State Hort. Soc.* 69: 357–360. 1957.*

CORRELL, D. S., & H. B. CORRELL. Flora of the Bahama Archipelago. 1692 pp. Vaduz. 1982. [Peperomiaceae, 404–407; key and descriptions of *Peperomia glabella* (illustr.), *P. magnoliifolia*, and *P. obtusifolia*.]

CRAIGHEAD, F. C. Orchids and other air plants of the Everglades National Park. 127 pp. Coral Gables, Florida. 1963. [Piperaceae, 109–112; *Peperomia glabella*, *P. humilis*, *P. obtusifolia*, and *P. simplex* keyed, described, and discussed.]

DAHLSTEDT, H. Studien über Süd- und Central-Amerikanische Peperomien. *Sv. Vet.-akad. Handl.* 33(2): 1–218. pls. 1–11. 1900. [Important reference concerning infrageneric classification of *Peperomia*; illustrations of fruits of numerous species, including many of those in our area.]

DASGUPTA, A., & P. C. DATTA. Karyological anatomy of root-tip of *Peperomia pellucida*. *Bull. Bot. Soc. Bengal* 33: 27–34. 1980. [Variation of chromosome numbers in somatic cells is studied, along with nuclear and cell volume.]

DATTA, P. C., & A. DASGUPTA. Root anatomy and distribution of common *Piper* and *Peperomia* species. *Geobios* 4: 143–146. 1977.*

DEFERRARI, A. M. Morfología foliar de especies argentinas del género *Peperomia* Ruiz & Pavón (Piperaceae). *Obra Cent. Mus. La Plata* 3: 63–96. 1977.*

DÜLL, R. Die *Peperomia*-Arten Afrikas. *Bot. Jahrb. Syst.* 93: 56–129. 1973. [Pertinent floristic study with key, descriptions, synonymy, and typification.]

FAGERLIND, F. Die Entwicklung des Embryosackes bei *Peperomia pellucida*. *Ark. Bot.* 29(17): 1–15. 3 tabs. 1940.

FISHER, G. C. Seed development in the genus *Peperomia*. *Bull. Torrey Bot. Club* 41: 137–156, 221–241. pls. 3–6. 1914. [Considers the 16-nucleate embryo-sac in *Peperomia* to be a derived condition.]

FRANCESCHI, V. R., & H. T. HORNER, JR. Calcium oxalate crystals in plants. *Bot. Rev.* 46: 361–427. 1980. [*Peperomia* spp. with druses in the palisade parenchyma of the leaf.]

HARRIS, G. P., & E. M. H. HART. Regeneration from leaf squares of *Peperomia Sandersii* A. DC.: a relationship between rooting and budding. *Ann. Bot.* II. 28: 509–526. 1964. [Bud and root initiation from leaf squares are dependent processes, similarly affected by various manipulations.]

HENSCHEN, S. Études sur le genre *Peperomia* comprenant les espèces de Caldas, Brésil. *Nova Acta Regiae Soc. Sci. Upsal.* III. 8: 1–53. 7 tabs. 1873. [Pertinent information concerning infrageneric categories; recognizes four sections of *Peperomia* for the species of this area.]

HILL, A. W. The morphology and seedling structure of the geophilous species of *Peperomia*, together with some views on the origin of monocotyledons. *Ann. Bot.* 20: 395–427. 1906.

———. A revision of the geophilous species of *Peperomia*, with some additional notes on their morphology and seedling structure. *Ibid.* 21: 139–160. 1907.

HOWARD, R. A. Notes on the Piperaceae of the Lesser Antilles. *Jour. Arnold Arb.* 54: 377–411. 1973. [Important taxonomic information concerning several species reported from our area (*Peperomia glabella*, *P. humilis* (as *Questeliana*), *P. magnoliifolia*, *P. obtusifolia*, and *P. pellucida*).]

———. Piperaceae. *Fl. Lesser Antilles* 4: 10–32. 1988. [Key and descriptions for six of the species reported in our area.]

- JOHNSON, D. S. On the endosperm and embryo of *Peperomia pellucida*. Bot. Gaz. 30: 1-11. pl. 1. 1900.
- . The germination of the seed of *Peperomia* and certain other genera. Johns Hopkins Univ. Circ. 21: 86. 1902.
- . A new type of embryo-sac in *Peperomia*. *Ibid.* 195: 1-7. 1907.*
- . Studies of the development of the Piperaceae. II. The structure and seed-development of *Peperomia hispidula*. Am. Jour. Bot. 1: 323-339, 357-397. 1914.
- JONES, A. G. An annotated catalogue of type specimens in the University of Illinois herbarium (ILL)—2. Piperaceae continued: *Arctottonia*, *Manekia* and *Peperomia*, plus some additions to Part 1 (*Piper*. Phytologia 59: 149-220. 1986.
- JOSE, J., & A. K. SHARMA. Chromosome studies in *Peperomia* Ruiz & Pav. Acta Bot. Indica 13: 77-83. 1985. [Base chromosome number eleven; karyotype analysis: *Peperomia magnoliifolia*, *P. obtusifolia*, and *P. pellucida* are included.]
- KAUL, R. B. The role of the multiple epidermis in foliar succulence of *Peperomia*. Bot. Gaz. 138: 213-218. 1977.
- KOTOVSHCHIKOVA, N. I. The structure of inflorescences in the genus *Peperomia* Ruiz & Pav. Sborn. Nauch. Tr. Nikit. Bot. Sada 97: 60-70. 1985.*
- KUHLMANN, M. Sinopse dos sub-gêneros de *Peperomia* Ruiz et Pav. Loefgrenia 82: 1-28. 1983. [Lists subgenera, sections, and species largely following DAHLSTEDT; illustrations of fruits.]
- KUO, C. M. *Peperomia pellucida* naturalized to Taiwan. Quart. Jour. Chinese Forest. 11: 123-128. 1978.*
- LEOGER, H. A. Descriptive flora of Puerto Rico and adjacent islands. Vol. 1. 353 pp. Puerto Rico. 1985. [Piperaceae, 16-34; several species of *Peperomia* reported from our area are keyed and described (*P. alata*, *P. emarginella*, *P. glabella*, *P. magnoliifolia*, *P. obtusifolia*, *P. pellucida*).]
- LONG, R. W., & O. LAKEA. A flora of tropical Florida. xvii + 962 pp. Miami. Florida. 1976. [Piperaceae, 341-344; includes key and brief descriptions of the six species of *Peperomia* recognized.]
- MCKENDRICK, M. The genus *Peperomia*: Taxonomy and cultivation. Plantsman 9: 163-189. 1987. [Excellent summary with detailed diagnoses of subgenera and sections following DAHLSTEDT; some illustrations of representative fruits; notes on cultivation and propagation included.]
- MADISON, M. An introduction to the peperomias. Marie Selby Bot. Gard. Bull. 3: 46. 1977. [Mentions *P. humilis* and *P. obtusifolia*.]
- MARTINOLI, G. Embriologia delle *Peperomia maculosa* Hook. Nuovo Giorn. Bot. Ital. 55: 235-250. 1948.
- MURTY, Y. S. Placentation in *Peperomia*. Phytomorphology 2: 132-134. 1952. [Study indicates that the seemingly basal position of the ovule is derived from a more primitive parietal placentation and that it should be correctly described as sub-basal.]
- . Studies in the order Piperales. II. A contribution to the study of vascular anatomy of the flower of *Peperomia*. Jour. Indian Bot. Soc. 37: 474-491. 1958. [Bicarpellate gynoecium suggested (pseudomonomerous).]
- . Studies in the order Piperales. III. A contribution to the study of floral morphology of some species of *Peperomia*. *Ibid.* 38: 120-139. 1959. [Describes developmental features associated with micro- and megasporogenesis for several species; variation in organization of the 16-nucleate embryo-sac noted.]
- . Studies in the order Piperales. I. A contribution to the study of vegetative anatomy of some species of *Peperomia*. Phytomorphology 10: 50-59. 1960. [Opposite and whorled leaf arrangements are derived from spiral.]
- NIKITICHEVA, Z. I., M. S. YAKOVLEV, & T. A. PLYUSHCH. The development of the ovule, embryo sac, and endosperm in the species of *Peperomia* (Piperaceae). (In Russian; English summary.) Bot. Zhur. 66: 1388-1398. 1981. [Includes

- P. obtusifolia* and *P. pellucida* as subjects; 3-celled egg apparatus is apparent, not 2-celled as commonly reported.]
- NOTOATMODJA, S. Comparative anatomy of Hawaiian *Peperomia* (Piperaceae) species. Ph.D. dissertation, University of Hawaii. 1967. [On the basis of chromosomal analysis and vegetative/floral anatomy, *Peperomia* is derived from *Piper* via simplification; whorled and opposite phyllotaxy are derived from spiral; unicarpellate gynoecium derived from tricarpellate.]
- PHILCOX, D. Flora of Trinidad and Tobago, vol. 2, part 8. Trinidad and Tobago. 1977. [Piperaceae, 506–553; key and descriptions of *Peperomia emarginella*, *P. glabella*, *P. obtusifolia* (syn. = *P. magnoliifolia*), and *P. pellucida*.]
- PLYUSHCH, T. A. Ultrastructure of *Peperomia blanda* L. (Piperaceae) embryo sac. (In Russian; English summary.) Ukrain. Bot. Zhur. 39(4): 88–91. 1982a.
- . Ultrastructure of *Peperomia blanda* L. (Piperaceae) embryo sac in the process of fertilization. (In Russian; English summary.) *Ibid.* 39(6): 30–36. 1982b.
- SASTRAPADJA, S. On the morphology of the flower in *Peperomia* (Piperaceae) species. Ann. Bogor. 4: 235–244. 1968a. [Pseudomonomerous gynoecium with tricarpellate ancestry is supported by reduction in number of stigmatic lobes and number of dorsal carpellary bundles.]
- . Chromosome study of Hawaiian *Peperomia* (Piperaceae) species. *Ibid.* 245–251. 1968b. [Base number 22; variations and meiotic irregularities, along with polyploidy, suggest that hybridization and polyploidy may be factors in speciation.]
- SMALL, J. K. The wild pepper-plants of continental United States. Jour. New York Bot. Gard. 32: 210–233. 1931. [Detailed historical account of *Peperomia* including habitat information for the five species that he recognized.]
- . Manual of the Southeastern flora. xxii + 1554 pp. New York. 1933. [Piperales, 399–402; five species of *Peperomia* keyed and described in the genera *Micropiper* and *Rhynchophorum*.]
- SMITH, C. W., & L.-F. LEW. Cellular arrangement in the nodes of various angiosperms. Bot. Gaz. 131: 269–272. 1970. [Several species of Hawaiian peperomias included in the analysis; discusses cell arrangement in relation to phyllotaxy.]
- SMITH, J. B. Chromosome numbers in *Peperomia* Ruiz & Pavón (Piperaceae) and a note on the chromosome number of *Piper magnificum* Trelease. Kew Bull. 20: 521–526. 1966. [Counts strongly suggest 11 as base number in *Peperomia*.]
- STARNECKER, G. Ökophysiologische Anpassungen im Gasstoffwechsel bei der Gattung *Peperomia* Ruiz & Pavón. 140 pp. Germany. 1984.
- TING, I. P., L. BATES, L. O. STERNBERG, & M. J. DENIRO. Physiological and isotonic aspects of photosynthesis in *Peperomia*. Pl. Physiol. 78: 246–249. 1985. [In general, the species investigated show characteristics of C₃ metabolism, not C₄ or CAM (crassulacean acid metabolism).]
- VIRZO DE SANTO, A., A. ALFANI, G. RUSSO & A. FIORETTO. Relationships between CAM and succulence in some species of Vitaceae and Piperaceae. Bot. Gaz. 144: 342–346. 1983. [For *Peperomia* species studied (only two), succulence is not causally related to CAM.]
- WUNDERLIN, R. P. Guide to the vascular plants of central Florida. viii + 472 pp. Florida. 1982. [Piperaceae, 157, 158; *Peperomia humilis*, *P. obtusifolia*, and *P. pellucida* recognized.]
- YUNCKER, T. G. The Cuban species of *Peperomia*. Revista Soc. Cubana Bot. 6(1): 5–33; 6(2-3): 20–54; 6(4): 9–34. 1950. [Key and descriptions of Cuban species, including *P. alata*, *P. emarginella*, *P. glabella*, *P. magnoliifolia*, *P. obtusifolia*, and *P. pellucida*.]
- . Piperaceae. Pp. 71–87 in A. L. STOFFERS, ed., Flora of the Netherland Antilles. Vol. II. Utrecht. 1966. [*Peperomia*, 76–87; key and descriptions of

several species reported from our area (*P. alata*, *P. emarginella*, *P. glabella*, *P. magnoliifolia*, and *P. pellucida*).]

———. The Piperaceae of Brazil: III. *Peperomia*; taxa of uncertain status. *Hoeheia* 4: 71-413. 1974. [Includes key to five subgenera recognized, each briefly described, and keys and descriptions of taxa reported in our area (*P. alata*, *P. emarginella*, *P. glabella*, *P. magnoliifolia*, *P. obtusifolia*, and *P. pellucida*).]

——— & W. D. GRAY. Anatomy of Hawaiian peperomias. *Occas. Pap. Bishop Mus.* 10: 1-19. 1934. [Detailed study of stem and leaf anatomy for several Hawaiian species, most of which are endemic; with illustrations.]

ZHITKOV, V. S. Formy fillotaksisa v rode *Peperomia* Ruiz et Pav. i osobennosti ikh morfogeneza. (Forms of phyllotaxis in the genus *Peperomia* Ruiz & Pavón and their morphogenesis.) *Biul. Moskovsk. Obsc. Isp. Prir. Otd. Biol.* 82: 103-119. 1977.*

THE ZAMIACEAE IN THE SOUTHEASTERN UNITED STATES¹

DENNIS WM. STEVENSON²

ZAMIACEAE Reichenbach, Handb. Nat. Pflanzensystems 139. 1837.

Stem subterranean [to arborescent, then often clothed in persistent leaf bases]. Leaves pinnately compound, in a crown of few (1-15) [to many (100+)]; pinnae 10-120 in subopposite to opposite pairs, articulated with [or decurrent on] rachis [often reduced to spines in lower region of rachis], densely pubescent when young, glabrous when mature, venation dichotomous [with or] without a midrib. Plants dioecious. Strobili cone-like, one to several, usually emerging from center

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project currently made possible through the support of National Science Foundation Grants BSR-8716834 (Norton G. Miller, principal investigator) and BSR-8717333 (Carroll E. Wood, Jr., principal investigator), under both of which this account was prepared. The 140th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39**: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of the family or genus in brackets [].

I thank Carroll Wood and Norton Miller for the opportunity to participate in the Generic Flora Project and for their editorial assistance, patience, and understanding during the production of this treatment.

The illustrations were drawn by Karen Stoutsenberger in 1978 under the supervision of Carroll Wood (who also prepared the dissections). Material for Figure 1, a-c was from preserved material obtained from the Carolina Biological Supply Company (exact source in Florida unknown). Figure 1, d-f was drawn in March 1978 from a plant grown at the Arnold Arboretum from a germinating seed collected in Marion County, Florida, and planted by Wood in April 1963. The ovulate strobilus was the first to be produced by this plant. Material for Figure 2 was collected by Wood and J. B. Fisher (a-l) and the author (m) in pinelands at the Montgomery Foundation, Fairchild Tropical Garden, Miami, Florida, in late July, 1977.

For loans of specimens, I thank the curators of the following herbaria: BM, BUFF, CAL, F, FTG, G, GOTT, HM, K, L, LE, MICH, MO, P, PHIL, U, UC, UM.

This work was also supported in part by National Science Foundation Grants DEB-7721495, DEB-7921130, BSR-8607049, and BSR-8796279 to the author.

²New York Botanical Garden, Bronx, New York 10458.

© President and Fellows of Harvard College, 1991.

Journal of the Arnold Arboretum, Supplementary Series 1: 367-384. 1991.

of crown; sporophylls [flat to] peltate. Microsporangiate strobili of numerous microsporophylls with sporangia located on the abaxial surface; microsporangia many, in groups of 2–5 and dehiscing by longitudinal slits; pollen monosulcate, proximal sculpturing foveolate [or fossulate or psilate]. Megasporangiate strobili of numerous ovule-bearing, stalked megasporophylls, each with two ovules. Seed coat when mature consisting of a red or orange/red [pink, white, or yellow] outer fleshy layer and an inner stony layer; megagametophyte farinaceous; embryo with two cotyledons and a coiled suspensor. TYPE GENUS: *Zamia* Linnaeus.

About 120 species in eight genera, in tropical to warm temperate regions of Africa, Australia, the West Indies, and North, South, and Central America. About 60 species in five genera occur in the Neotropics (Stevenson *et al.*, 1990).

Although the Zamiaceae were first separated from the Cycadaceae in 1837 (Reichenbach), the acceptance of the family thereafter was sporadic. Prior to the work of Johnson in 1959 only Haeckel in 1894 and Wettstein in 1907 recognized the group as a distinct family. The Zamiaceae comprise eight of the 11 extant genera of cycads and are currently understood to be composed of two subfamilies, the Zamioideae and Encephalartoideae D. Stevenson, each with four genera (Stevenson, 1990b). Autapomorphies (uniquely derived characters) of the Encephalartoideae include anastomosing leaflet venation, leaflets reduced proximally to spines, and the presence of cataphylls on strobilar peduncles. In contrast, autapomorphies of the Zamioideae include small stipulelike outgrowths on the leaf base, articulated leaflets, and truly peltate sporophylls. The Encephalartoideae include *Dioön* Lindley, a Central American genus of 10 species (Sabato & De Luca); *Encephalartos* Lehm., a South, Central, and West African genus of approximately 50 species (Goode); and *Lepidozamia* Regel and *Macrozamia* Miq., Australian endemics with two and 14 species, respectively (Johnson). The Zamioideae contain *Ceratozamia* Brongn., with 10 species occurring in an area from Central Mexico to Belize and Guatemala (Stevenson *et al.*, 1986); *Chigua* D. Stevenson, with two species limited to a small area of northern Colombia (Stevenson, 1990c); *Microcycas* (Miq.) A. DC., a monotypic Cuban endemic; and *Zamia* L., a genus distributed throughout the Neotropics and consisting of approximately 40 species.

The history of classification systems for the Cycadales has been summarized by Johnson and by Stevenson (1990b). Thus, only the more salient features regarding the placement of *Zamia* within the Zamioideae will be discussed here.

In general, cycad genera are easily recognized by reproductive characters, particularly general strobilar morphology, and vegetative characters such as leaf morphology. However, exceptions are found in the Zamioideae. For example, *Ceratozamia* with its two distinctive horns on each sporophyll is unique among cycad genera, but on the basis of leaf morphology it is indistinguishable from many species of *Zamia*.

The strobili and leaves of *Microcycas* are similar to those of *Zamia*. In fact, *Microcycas calocoma* (Miq.) A. DC. was originally described as a species of *Zamia* (Miquel, 1852). Eckenwalder (1980a) suggested that *Microcycas* could be placed in *Zamia*, citing differences exhibited by *Microcycas*, including a flattened knob on the end of the microsporophylls, megagametophytes with many archegonia, and microgametophytes that produce numerous male gametes. However, Stevenson (1990b) pointed out that there are other gross morphological features of the megasporophylls and leaves that separate *Microcycas* from *Zamia*, including truncated leaves and most megasporophylls bearing a terminal cleft. In contrast, the most prominent autapomorphy of *Zamia* is the hexagonal sporophyll tips, which have six inclined facets surrounding a central facet. Finally, the recently discovered genus *Chigua* Stevenson (1990c), has both vegetative and reproductive autapomorphies, including leaflets with a midrib and a raised area at each angle of the hexagonally shaped sporophyll tips, which lack lateral facets.

Relationships within the Zamioideae are not yet clear because the character states for many anatomical and chemical features are not known for *Chigua* (Stevenson, 1990b). However, our current limited knowledge of *Chigua* indicates that this genus is in all probability most closely related to *Zamia* (Stevenson & Siniscalco Gigliano; Stevenson, 1990b, c). Besides the similarities of *Chigua* to *Zamia* in overall leaflet and strobilus morphology, there are chemical similarities in the monosaccharide composition of their mucilages (Stevenson & Siniscalco Gigliano). The distribution patterns of hydrolysed monosaccharides in cycad mucilages are reliable generic markers, and infrageneric and infraspecific variability occurs only with respect to the total percentage of monosaccharides in the mucilage. Only two genera, *Chigua* and *Zamia*, exhibit a remotely similar distribution pattern of mucilage monosaccharides (Stevenson & Siniscalco Gigliano), thus supporting their close relationship.

Recent work on pollen morphology has done surprisingly little to clarify the relationships among the cycads, partly because there is little variability and partly because of discrepancies between the observations of various authors (Audran & Masure; Dehgan & Dehgan; Marshall *et al.*). In the paper by Dehgan & Dehgan, the photographs in some cases do not match the descriptions and tables, confounding the situation even more. Apparently, these authors have reversed the usage of standard terminology and based descriptions on distal instead of proximal views of the pollen grains. The descriptions of Audran & Masure and of Marshall *et al.* are in agreement. Within the Zamioideae, the pollen sculpturing is foveolate. In *Ceratozamia* and *Zamia* it is coarsely foveolate and in *Microcycas* very finely foveolate. *Chigua* also has coarsely foveolate pollen grains (Stevenson, unpubl. obs.). Only *Microcycas* has distinct pollen sculpturing that supports its recognition at the generic level.

Cycads are not economically important plants, although the stems and seeds are often used as a source of starch after washing and roasting

to remove toxic compounds. Some species, particularly *Cycas revoluta* Thunb., are known as sago palm and are grown in greenhouses and outdoors in appropriate climates. *Cycas circinalis* and other species, for example, *Ceratozamia Hildae* Landry & M. Wilson, *Dioon edule* Lindl., *Zamia furfuracea* L. f. ex Aiton, and *Z. pumila* L. are becoming more important horticulturally (see Bailey *et al.*). Of interest is the implication that *C. circinalis* is responsible for the precocious development of neurological disorders such as Parkinsonism dementia and amyotrophic lateral sclerosis in Guam (Kurland).

REFERENCES:

- AUDRAN, J., & E. MASURE. Contribution à la connaissance de la composition des sporodermes chez les Cycadales (Prespermaphytes). Étude en microscopie électronique à transmission (M.E.T.) et à balayage (M.E.B.). *Palaeontographica* 162: 115–158. 1977. [A survey of 25 species representing seven genera.]
- BAILEY, L. H., E. Z. BAILEY, & L. H. BAILEY HORTORIUM STAFF. Hortus third. xiv + 1290 pp. New York & London. 1976. [Cycadaceae, 349, 350; Zamiaceae, *Zamia* (8 spp.), 1180; "all genera of cycads are represented in cultivation." (p. 350).]
- CANDOLLE, A. DE. Cycadaceae (Tribus Zamieae Miq.). DC. Prodr. 16(2): 537–546. 1868. [One family with nine genera and 54 species.]
- CHAMBERLAIN, C. J. The living cycads. xiv + 172 pp. Chicago. 1919. [The best general account of cycad biology.]
- DEHGAN, B., & N. DEHGAN. Comparative pollen morphology and taxonomic affinities in the Cycadales. *Am. Jour. Bot.* 75: 1501–1516. 1988. [A survey of 29 species representing 10 genera.]
- ECKENWALDER, J. Taxonomy of the West Indian cycads. *Jour. Arnold Arb.* 61: 701–722. 1980a. [Nomenclature and typification of names of species; only *Zamia pumila* and *Microcycas calocoma* recognized as species.]
- . Dispersal of the West Indian cycad, *Zamia pumila* L. *Biotropica* 12: 79, 80. 1980b.
- HAECKEL, E. Systematische Phylogenie der Protisten und Pflanzen. xvi + 400 pp. Berlin. 1894.
- GIDDY, C. Cycads of South Africa. 122 pp. [incl. 30 pls. colored photographs]. Pencil drawings by BARBARA JEPPE. Cape Town. 1974. [*Stangeria eriopus*, *Encephalartos* (28 spp.).]
- GOODE, D. Cycads of Africa. 256 pp. Cape Town. 1989. [Three genera (*Cycas*, *Stangeria*, *Encephalartos*); 53 species; detailed paintings and drawings of all species; selected bibliography].
- JOHNSON, L. A. S. The families of cycads and the Zamiaceae of Australia. *Proc. Linn. Soc. New S. Wales* 84: 64–117. 1959. [Ten genera in three families; only Australian species included; *Stangeriaceae* fam. nov.]
- KURLAND, L. *Cycas circinalis* as an etiologic risk factor in amyotrophic lateral sclerosis and other neurodegenerative diseases on Guam. Proceedings of the Second International Conference on Cycad Biology, Palm and Cycad Society of Australia. Milton, New S. Wales. (In press.) 1991.
- MARSHALL, J., N. GROBBELAAR, J. COETZEE, & R. OSBORNE. Pollen morphology of the Cycadales with special reference to the *Encephalartos* species. *Pollen Spores* 31: 229–249. 1989. [A survey of 62 species representing 10 genera.]
- MIQUEL, F. A. W. Sur une espèce nouvelle de *Zamia* des Indes Occidentales, introduite dans l'établissement Van Houtte, à Gand. *Flore des serres et des jardins de l'Europe* 7: 141, 142. 1852.
- . *Prodromus systematis cycadearum*. 36 pp. Amsterdam. 1861.

- PANT, D. D., & D. D. NAUTIL. Cuticle and epidermis of recent Cycadales. Leaves, sporangia and seeds. *Senck. Biol.* **44**: 257–347. 1963. [Incl. *Zamia integrifolia* (as *Z. floridana*).]
- REICHENBACH, H. G. L. Handbuch der natürlichen Pflanzensystems. x + 346. Dresden & Leipzig. 1837.
- SABATO, S., & P. DE LUCA. Evolutionary trends in *Dion* (Zamiaceae). *Am. Jour. Bot.* **72**: 1353–1363. 1985. [*Dioön*, orth. cons.; incl. key to species.]
- SCHUSTER, J. Cycadaceae. In: A. ENGLER, Das Pflanzenreich IV. 1 (Heft 99): 1–168. 1932. [One family with nine genera, 69 species.]
- STEVENSON, D. W. Observations on ptyxis, phenology, and trichomes in the Cycadales and their systematic implications. *Am. Jour. Bot.* **68**: 1104–1114. 1981. [Ten genera in four families; Boweniaceae, *fam. nov.*]
- , ed. The biology, structure, and systematics of the Cycadales. *Mem. New York Bot. Gard.* **57**: vii + 1–102. 1990a. [Twenty-two diverse papers, many of them cited here; indices to common names and scientific names.]
- . Morphology and systematics of the Cycadales. *Ibid.* 8–55. 1990b. [Review paper with cladistic analysis and extensive bibliography.]
- . *Chigua*, a new genus in the Zamiaceae with comments on its biogeographic significance. *Ibid.* 169–172. 1990c.
- , R. OSBORNE, & J. HENDRICKS. A world list of cycads. *Ibid.* 200–206. 1990. [Four families with 11 genera and 143 species.]
- , S. SABATO, & M. VAZQUEZ TORRES. A new species of *Ceratozamia* (Zamiaceae) from Veracruz, Mexico with comments on species relationships, habitats, and vegetative morphology in *Ceratozamia*. *Brittonia* **38**: 17–26. 1986. [Incl. key to species; *C. euryphyllidia*, sp. nov.]
- & G. SINISCALCO GIGLIANO. The systematic value of the monosaccharide composition and distribution pattern of cycad mucilages. *Biochem. Syst. Ecol.* **17**: 185–190. 1989. [Monosaccharide profile of mucilage distinct at generic level and consistent between vegetative and reproductive parts.]
- WETTSTEIN, R. Handbuch der systematischen Botanik **2**: 161–394. Leipzig & Wein. 1907.

1. *Zamia* Linnaeus, Sp. Pl. ed. 2. **2**: 1659. 1763, nom. cons.; Gen. Pl. ed. 6. 574. 1764.

Stems subterranean and tuberous [or trunk to 5 m], 3–10 [25] cm in diameter, often dichotomously branched, wrinkled [smooth] and devoid of old leaf bases. Cataphylls alternating with leaves, from 1–2 [6] cm long, sheathing at first, with a pair of inconspicuous stipules. Leaves generally few (2–15); petioles with stipules, smooth [or armed with scattered prickles]. Rachis bearing 5–30 [60] pairs of opposite to subopposite leaflets, smooth [or armed with scattered prickles in lower third to two-thirds], ending in a terminal acute spine. Leaflets [linear to] oblong [to broadly ovate], 8–25 [2–45] cm long and 0.5–2 [0.2–30] cm wide, sessile [to petiolulate, with or without a collar-shaped gland], rounded [to long acuminate] apically, with 10–15 indistinct teeth in upper fourth [or margin entire or more commonly serrate in upper half]. Microsporangiate (pollen) strobili pedunculate, [cream colored to] dark reddish brown [or black], 1–30, emerging from center of leaf crown, cylindrical but gradually tapering towards acute [to acuminate] apex, each 3–15 [1–30] cm long and 0.8–2 [0.5–8] cm in diameter, densely pubescent; microsporophylls obscurely peltate, 0.5–1 [0.2–1.5] cm long,

8-64 abaxial microsporangia [with rarely a few adaxially] in clusters of 2-4; pollen exine foveolate. Megasporangiate (ovulate) strobili pedunculate, tomentose, [cream to] dark reddish brown [or rarely green], usually solitary but occasionally up to 3, emerging from center of leaf crown, cylindrical to slightly ovoid, with blunt or slightly acute apex, each 6-15 [2.5-55] cm long and 4-6 [1.5-20] cm in diameter, densely pubescent [or glabrous]; megasporophylls arranged in 5-8 vertical orthostichies, the exposed tips thick, truncate, hexagonal, with six lateral facets surrounding a central prominent [depressed] facet, each bearing two lateral ovules. Seeds with a red to orange-red [or pink or yellow] sarcotesta and a stony endotesta, ovoid, 1-2 [0.5-2.5] cm long. Chromosome numbers $2n = 16$, [18, 19, 22, 23, 24, 25, 26, 27, 28]. (*Palma-filix* Adanson, nom. rejic.; *Aulacophyllum* Regel.) TYPE SPECIES: *Zamia pumila* L., the only species at the founding of the genus. (Name from Latin, *zamia* [Greek, *zemia*], loss or damage, applied by Pliny to the strobilus (cone) of *Pinus*, which he thought damaged the next crop if left to decay on the tree; adopted by Linnaeus for this cycad with its analogous strobilus, which he compared with that of *Cupressus*. See Linnaeus, Gen. Pl. ed. 6. 574. 1764, Syst. Nat. ed. 12. 2: 731. 1767; G. R. Boehmer, Lexicon Rei Herbariae. p. 214. 1802.)

A genus of about 40 species represented sporadically throughout the Neotropics, but some species native beyond (e.g., Georgia and Florida, Bolivia). Most species are narrow endemics, although a few are more widespread. The plants generally grow in undisturbed primary forest at elevations from sea level to 2500 m.

In our area, only *Zamia integrifolia* L. f. ex Aiton (*Z. floridana* A. DC., *Z. angustifolia* Jacquin var. *floridana* (A. DC.) Regel, *Z. floridana* var. *Purshiana* Schuster, *Z. floridana* var. *Purshiana* forma *silvicola* (Small) Schuster, *Z. erosa* Cook & Collins, *Z. lucayana* Britton, *Z. media* Jacquin, *Z. tenuis* Willdenow, *Z. media* var. *tenuis* (Willd.) Schuster, *Z. silvicola* Small, *Z. umbrosa* Small), $2n = 16$. Florida arrowroot, Seminole bread, coontie, occurs from extreme southeastern Georgia through peninsular Florida and the Florida Keys. Eckenwalder (1980a) included *Z. integrifolia* in his broad concept of *Z. pumila* subsp. *pumila*, but *Z. integrifolia* is recognized here as a distinct species (see discussion below).

Zamia is ecologically, morphologically, and karyologically the most diverse of the cycad genera. Most species occur on dry soils. When in wet areas, they are usually on well-drained sites or rocky slopes. However, there are exceptions such as the epiphytic *Z. pseudoparasitica* Yates (Panama) and the salt-tolerant *Z. Roezlii* Linden that can grow in mangrove swamps (Colombia). Some species are found in the Amazonian rainforest but usually on the sides of small, rocky mountains where the plants appear to do well in contrast to their paucity in the wet understory. In general, species such as *Z. obliqua* A. Braun that tolerate wet habitats have well-developed trunks. All species have ageotropic coralloid roots that contain nitrogen-fixing cyanobacteria

(blue-green algae). The greatest development of these coralloid roots appears in the epiphytic *Z. pseudoparasitica* in which the root masses are hemispherical and up to 25 cm in diameter.

General growth habit in *Zamia* ranges from species with small, smooth, subterranean stems (e.g., *Z. pygmaea* Sims or *Z. Fischeri* Miquel) to species with tall (to 5 m), columnar stems (e.g., *Z. obliqua*, *Z. Roezlii*, or *Z. Skinneri* Warscz. ex A. Dietr.). Stems of the latter type may be either smooth and slender (10–12 cm), as in *Z. obliqua*, or have subsistent leaf bases and considerable thickness (to 25 cm) as in *Z. Roezlii*. In species without aerial trunks, the stems remain underground as a result of taproot and stem contraction (Stevenson, 1980a). Since axillary buds are not present in the cycads, branching is uncommon, but three types of vegetative branching do occur: apical dichotomies, adventitious buds formed from leaf-base callus, and adventitious buds formed from lateral meristems near points of injury (Stevenson, 1988). The amount of secondary wood is generally a small part of the stem, which is composed mainly of a large parenchymatous pith and a broad cortex derived from a primary thickening meristem (Stevenson, 1980b). Consequently, species of *Zamia* are pachycaulous, as are all cycads. Unlike some genera, such as *Cycas*, polyxylic secondary growth does not occur in *Zamia*.

Leaf morphology and production are variable in *Zamia*. The only feature of leaf morphology that is correlated with stem habit is the shape (ptyxis) of the emerging leaves. In general, species with subterranean axes (such as *Z. integrifolia*) have inflexed ptyxis, in contrast to species with well-developed trunks (such as *Z. obliqua*) that have erect ptyxis (Stevenson, 1981). All species of *Zamia* produce one annual flush containing from one to thirty or more leaves. The production of a single annual leaf appears to be limited to a few, but not all, species with subterranean stems (e.g., *Z. Wallisii* A. Braun).

The leaflets are articulated with the rachis. Venation is open and dichotomous. Leaflets of some species have entire margins, while in others leaflets have distinct marginal teeth. The teeth may be inconspicuous and restricted to the apical region, as in *Z. integrifolia*, or may be well developed and occur all along the leaflet margins, as in *Z. Poepigiana* Martius & Eichler. Leaflet texture varies from extremely coriaceous (*Z. inermis* Vovides, Rees & Vazquez Torres) to almost membranaceous (*Z. Fisheri*). Most species of *Zamia* have flat, smooth leaflets, but a few species, such as *Z. Skinneri* and *Z. Wallisii*, have leaflets that are deeply grooved adaxially between the veins. This character was used to segregate the genus *Aulacophyllum* Regel (1876). It appears, however, not to be correlated with any other characters, and not all species of *Zamia* included by Regel in *Aulacophyllum* have this type of leaflet. In general, the leaflets are sessile, but in some species there is a distinct petiolule, e.g., *Z. Wallisii* and *Z. manicata* Linden ex Regel. The latter species is very unusual in the Cycadales because there is a conspicuous adaxial, semicircular, gland-like structure

of unknown function at the junction of the lamina and the petiolule (Stevenson, 1990b).

As in all cycads, the species of *Zamia* are dioecious. In comparison with the variability found in vegetative morphology, strobilus morphology is more constant, much of the variation being in the size and color of strobili and in the shape of the terminal portions of the sporophylls. Strobilus color varies from black in *Z. angustifolia* Jacquin to tan in many species to yellow-tan in *Z. obliqua* to dark red-brown in *Z. boliviana* (Brongn.) A. DC. Generally, microsporangiate and ovulate strobili are the same color within a species. However, there are exceptions such as *Z. Tuerckheimii* J. Donnell-Smith, which has tan microsporangiate strobili and green ovulate ones. Microsporangiate strobili vary in size at maturity from 1 cm long in an as yet undescribed species from South America to 30 cm long in *Z. Fairchildiana* L. D. Gomez. Ovulate strobili vary in length from 2.5 cm when mature in *Z. pygmaea* to more than 50 cm long in *Z. Poeppigiana*. All sporophylls are peltate, with the expanded tip composed of a terminal facet surrounded by six inclined facets. In most species, the six facets surrounding the terminal one are only slightly inclined. In other species, such as *Z. obliqua*, the tip, particularly apparent in the microsporophylls, appears very distinctly pyramidal because the six surrounding facets are steeply inclined and the terminal one is smaller than the lateral facets.

Generally in cycads, microsporangia are found only on the abaxial surface of the microsporophylls. However, in at least four species of *Zamia*, including *Z. obliqua* and three undescribed species, both adaxial and abaxial microsporangia are present (Stevenson, unpubl. obs.). However, the adaxial microsporangia are few and located only in one or two rows adjacent to the sterile tip. In the species of *Zamia* that have been examined, pollen sculpturing is foveolate (Audran & Masure; Dehgan & Dehgan; Marshall *et al.*).

Cycad genera are remarkably uniform cytologically, with the exception of *Zamia* (Moretti, 1990a, b). All North American and West Indian plants that have been examined are $2n = 16$ (Norstog, 1980; Moretti, 1990a). In striking contrast, the diploid number in Central and South American species is quite variable both between and within species (Moretti, 1990a, b; Norstog, 1980, 1981). Diploid numbers are also variable within a population (Moretti & Sabato, 1984; Moretti, 1990a, b; Norstog, 1980, 1981). Even more remarkably, all plants of some populations of *Z. paucijuga* Wieland (e.g., on Isla Maria Cleofas, Nayarit, Mexico, $2n = 27$) appear to have an odd diploid number (Moretti & Sabato, 1984; Moretti, 1990a, b), even though these populations do not contain apomictic plants and consist of seedlings and plants of varying age (i.e., the populations presumably are sexually reproductive).

Variation in diploid chromosome number within and among populations of a species can be better understood from the relative difference in the numbers of metacentric versus telocentric chromosomes. For example, in *Z. paucijuga* there is a series of karyotypes, $2n = 23, 24, 25$,

26, 27, and 28. All of these karyotypes have two submetacentric and two acrocentric chromosomes and differ only in the number of metacentric (M) and telocentric (T) chromosomes. For example, in the $2n = 23$ karyotype there are 5 M and 14 T chromosomes, whereas the $2n = 24$ karyotype has 4 M and 16 T. For each increase in diploid number there is a corresponding decrease of one metacentric chromosome and a corresponding increase of two telocentric chromosomes. This has been interpreted as Robertsonian fusion of two telocentrics to form one corresponding metacentric (Norstog, 1980) and as Robertsonian fission of each metacentric to form two corresponding telocentrics (Moretti 1990a, b). Regardless of the interpretation as fusion or fission, therein lies the explanation of populations composed of individuals of differing diploid numbers.

Insect pollination in the cycads was first unequivocally demonstrated in the Mexican *Zamia furfuracea* L. f. ex Aiton (Norstog *et al.*) and has since been demonstrated for *Z. integrifolia* in Florida by Tang (1987a). In both cases, pollination is by curculionid (snout) weevils of the genus *Rhopalotria* and by a clavicorn beetle, *Pharaxonotha zamiae*. Different species of *Rhopalotria* are associated with these two species of *Zamia*, viz., *R. mollis* is a pollinator of *Z. furfuracea* and *R. slossoni* is a pollinator of *Z. integrifolia*. Recently, Fawcett, Norstog, & Stevenson (unpubl. obs.) have also found *R. slossoni* associated with *Z. integrifolia* on New Providence Island, Bahamas. Other species of *Zamia* may be pollinated by snout weevils and clavicorn beetles as well, and *R. bicolor* and *Pharaxonotha* sp. have been found in pollen "cones" of *Ceratozamia* and *Dioön* (Vovides); *Rhopalotria dimidata* appears to be associated with *Z. pygmaea* in Cuba, and an unidentified species of *Rhopalotria* is associated with *Z. inermis* in Mexico (Vovides, pers. com.) and with *Z. Loddigesii* Miq., *Z. Fairchildiana*, and *Z. muricata* Willd. in Mexico, Panama, and Venezuela, respectively (Fawcett, Norstog, & Stevenson, unpubl. obs.). In all of these cases and many others, *Pharaxonotha* has also been found (Fawcett, Norstog, & Stevenson, unpubl. obs.). Further studies by Norstog & Fawcett (1989) demonstrated that *R. mollis* and *Z. furfuracea* are symbiotic. They have shown that breeding, larval stages, and pupation in this snout weevil occur during pollen-cone development. Moreover, some of the pupae undergo the diapause phase and emerge as adults when the pollen strobili of the next season develop. The adult weevils copulate and oviposit on the growing pollen cones, and the resulting larvae complete their cycle in the cones with some larvae going into diapause. The case of *P. zamiae* is less obligate, and these beetles, besides being less effective pollinators, are also able to utilize other food sources, e.g., palm pollen.

Tang (1987a) demonstrated effective pollination in *Zamia integrifolia* by *Rhopalotria mollis* and *Pharaxonotha zamiae*. He (1987b) has also shown that both pollen and seed strobili have a daily thermogenic cycle during elongation, when the pollen is shed, and at the time of pollination. The thermogenic cycle is correlated with odor production

by the cones. In some instances the fragrances appear to be similar or the same as those produced by some angiosperms (Pellmyr *et al.*). The odors seem to attract *Rhopalotria* adults to *Zamia* cones and possibly to play a role in releasing larvae from diapause. *Rhopalotria* larvae collected and stored while in diapause were observed to be released from diapause when maturing pollen cones were brought into the laboratory (Fawcett, pers. com.). Further studies by Fawcett & Norstog (1991) have demonstrated that as in the *Z. furfuracea*-*R. mollis* symbiosis, there is also a *Z. integrifolia*-*R. slosoni* symbiosis.

The case with *Pharaxonotha zamiae* remains enigmatic because this beetle spends time on other plants, is more general in its food selection, has its diapause period in the soil, and apparently does not copulate on pollen cones of *Zamia integrifolia*. In both *Zamia* species, snout weevils and clavicorn beetles do not interfere with each other because they have a tendency to occupy and utilize different regions of the pollen cone and have slightly different timing in their life cycles (Norstog & Fawcett; Fawcett & Norstog). *Rhopalotria slosoni* prefers sporophylls at the base of the pollen cone, whereas *P. zamiae* prefers sporophylls at the top of the pollen cone (Fawcett & Norstog). Also, *Pharaxonotha* lays its eggs some time after *Rhopalotria* oviposits, so that the larvae of the weevil start to pupate when the larvae of the beetle are young. One of the more interesting observations about insect pollination in *Zamia* is that in northern Florida *Rhopalotria* is absent (although there are historical records of its presence), and pollination is effected by *Pharaxonotha* alone. This led Fawcett & Norstog to conclude that *Rhopalotria* has become extinct in this area, which may have important consequences for reproduction in populations of *Zamia* there.

These observations, combined with the fact that the curculionids are primitive beetles with a fossil record beginning in the Carboniferous and are also associated with the Mesozoic Bennettitales, suggest that insect pollination was well developed before the evolution of the angiosperms. It would appear that these insect pollinators have evolved along with cycads because all parts of the cycad plant, except the fleshy seed coat, contain highly toxic compounds. Perhaps the most interesting toxic compound in cycads is the non-protein amino acid neurotoxin 2-amino-3-(methylamino)propanoic acid (BMAA). Present in the tissues upon which the larvae feed, BMAA would be incorporated into proteins, causing tertiary protein configuration to be disrupted or changed in such a way that the insects would fail to pupate or metamorphose normally. Thus, these insects have evolved a process to either sequester BMAA or detoxify it, because no such failure to pupate occurs in either the snout weevils or clavicorn beetles that feed on cycads as larvae. Furthermore, since different weevil species are associated with different cycad species, at least some weevils must have evolved with cycads at the level of species.

The taxonomy of the West Indian species of *Zamia*, of which our native species is but one element, has been clouded with vagaries from the beginning (Eckenwalder, 1980a; Stevenson, 1987a, b). The extremes

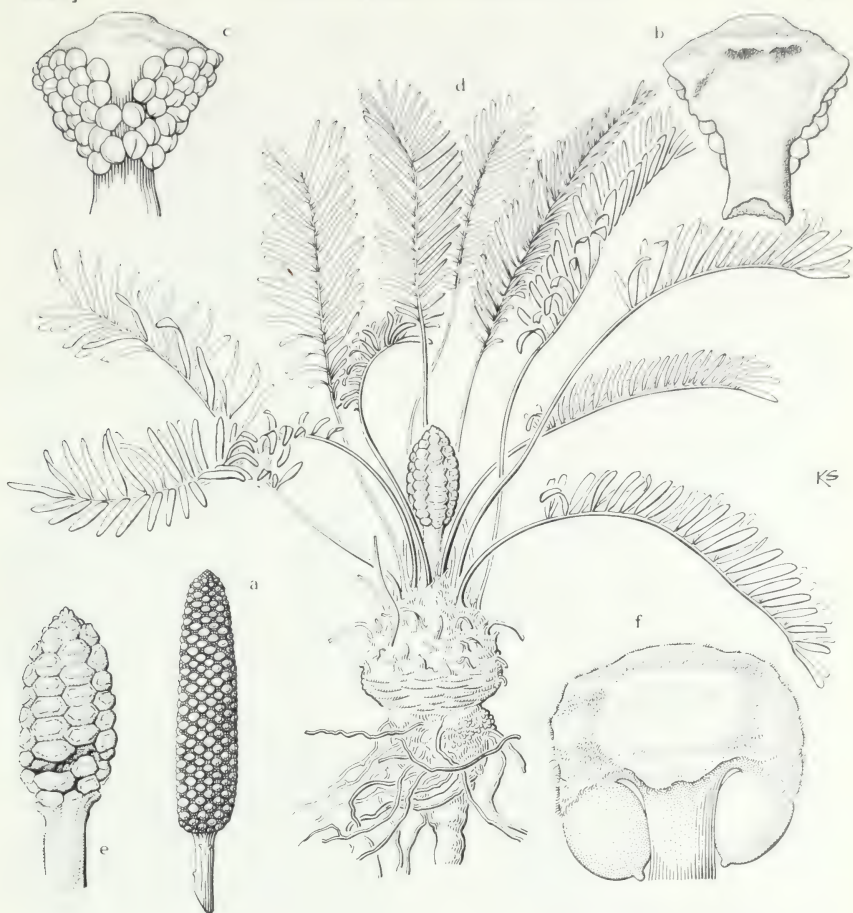


FIGURE 1. *Zamia*. a-f, *Z. integrifolia*: a, microsporangiate strobilus during pollen shedding, $\times 3/8$; b, adaxial surface of microsporophyll, $\times 3$; c, abaxial surface of microsporophyll with microsporangia, $\times 3$; d, habit of ovulate plant (some leaves removed) with strobilus at time of pollination and large fleshy tap root with small lateral roots and coraloid roots (shown at right near the stem-root juncture), $\times 1/2$; e, ovulate strobilus at time of pollination—note separation of megasporophylls in lower portion of strobilus allowing entry of pollinators and pollen, $\times 1/2$; f, adaxial view of megasporophyll with two ovules, each with micropyle directed towards axis at bottom, $\times 3$.

range from the recognition of 14 or more species (De Candolle) to one species with two subspecies for the entire region (Eckenwalder, 1980a). In Florida alone, Small (1933) recognized four species. The recognition of several species in the West Indies and Florida has usually rested upon leaflet width and number of veins per leaflet coupled with geographical criteria. In an over-simplified sense, a different species has been thought to occupy a different island or habitat. Eckenwalder (1980a) demonstrated that as leaflets increase in width the number of veins also

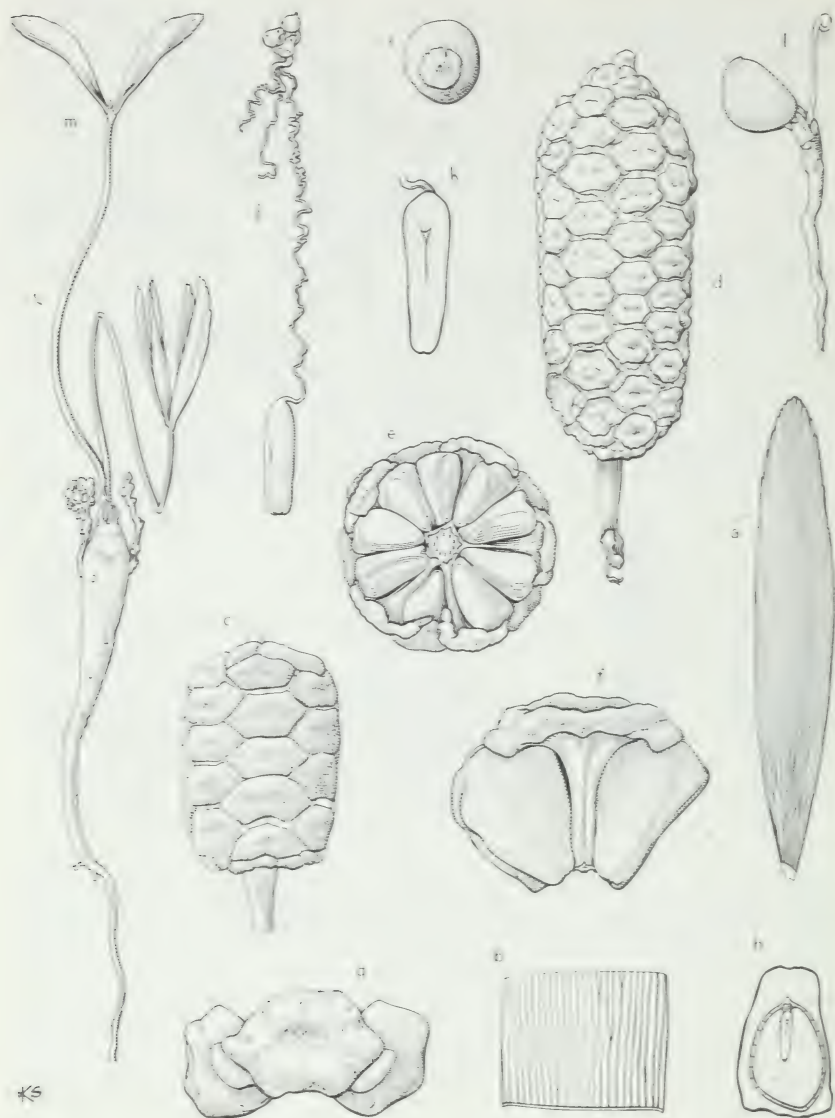


FIGURE 2. *Zamia*. a-m, *Zamia integrifolia* (continued): a, leaflet, $\times 1$; b, portion of lower half of leaflet with details of dichotomous venation pattern, $\times 2$; c, ovulate strobilus with maturing seeds, $\times 3/8$; d, large mature ovulate strobilus just before shedding of mature seeds—note shrivelled megasporophylls, $\times 3/8$; e, cross sectional view of mature strobilus, showing relationships of mature seeds, megasporophylls, and strobilus axis, $\times 1/2$; f, adaxial view of mature megasporophyll and seeds, $\times 1$; g, end view of megasporophyll with two mature seeds, adaxial surface at the top, $\times 1$; h, diagrammatic longitudinal section of mature seed (micropyle pointing up)

increases. As a result of this and some other factors such as a uniform karyotype throughout the West Indies, Eckenwalder (1980a) accepted only one species, *Z. pumila* L. composed of subsp. *pumila* and subsp. *pygmaea* (Sims) Eckenwalder, based upon general plant size and leaflet shape. As pointed out by Stevenson (1987a, b) and Sabato (1990), this approach ignores the correlation of some more general aspects of leaflet morphology such as shape and distribution of marginal teeth and strobilus color and shape. Consequently, these authors recognize six and five species, respectively, for the West Indies; the distribution of characters and keys can be found in their works. More recently, Walters & Decker-Walters have analyzed allozyme diversity in West Indian and Floridian species of *Zamia*. Only *Z. angustifolia* was found to be distinct from all others in allozyme pattern. Thus, this approach like all others applied to date has not resolved the species-level taxonomy of *Zamia* in the West Indies.

In the southeastern United States only one species is recognized, *Zamia integrifolia*. Although there is some local variation and also variation between sun and shade plants with respect to leaf length and leaflet size and texture, it is not possible to correlate this variation with other variables such as strobilus morphology or general leaf morphology. In fact, the type specimens of species described from plants collected in Florida and accepted by Small (1933), *Z. integrifolia*, *Z. floridana* A. DC., *Z. silvicola* Small, and *Z. umbrosa* Small, are basically identical. It is to be suspected that some of the local variation has developed as a result of the disjunct distribution of local populations and a reduction in gene flow between them. The presence of insect pollinators and seed dispersal indicates that speciation probably will not occur as long as some gene flow is maintained. However, the results of human activities such as the removal of pollinators and destruction of *Zamia* populations, and the inability to disperse significantly from the parent populations negatively affects gene flow.

Zamia integrifolia is known from extreme southeastern Georgia southward through peninsular Florida (including the Florida Keys) and sporadically in the Bahamas where it occurs on Andros, Grand

with embryo, sarcotesta unshaded, sclerotesta hatched, megagametophyte stippled, embryo unshaded, with radicle and coiled suspensor at top and apically fused cotyledons below, $\times 1$; i, micropylar view of megagametophyte, seed coat removed, sporangial remains forming a cap over megagametophyte, pollen chamber appearing as a central depression, $\times 1$; j, embryo and two aborted embryos with their suspensors uncoiled and remains of the three archegonia appearing as balloon-like remains at top, $\times 2$; k, longitudinal section of embryo with radicle and part of suspensor up (as in "j") and the two partially fused cotyledons down, $\times 3$; l, germinated seed with primary tap root, two fused haustorial cotyledons remaining embedded in megagametophyte (this enclosed in sclerotesta, sarcotesta rotted away), and first inflexed leaf emergent between free parts of cotyledons, $\times 3/4$; m, older seedling with bases of leaves 1 and 2 visible and leaves 3 and 4 with two and four leaflets respectively, carrot-like primary root with two lateral ageotropic coralloid roots with cyanobacteria (blue-green algae), $\times 3/4$.

Bahama, Great Abaco, Long, and New Providence Islands. It has been collected in Cuba, the Cayman Islands, and south-central Puerto Rico (where it may now be extinct). Habitats vary from open coastal areas and sand dunes to pinelands and closed-canopy oak hammocks to tropical forest. This cycad is most commonly found in soil over limestone and in sand near sea level or in pinelands subjected to periodic wildfires.

Much of the natural history of *Zamia integrifolia* in South Florida has been investigated in a series of recent studies (under the name *Z. pumila*) by Tang (1987a, b; 1989; 1991). Prior to this, most studies were mainly concerned with detailed aspects of strobilus morphology (Smith 1907, 1910, 1929), elegant investigations into the details of the microgametophyte and fertilization (Webber, 1897a-c, 1901; and Norstog, 1967, 1968, 1972, 1974, 1975), developmental anatomy (Johnson 1939, 1943), taxonomic and distributional problems (Small, 1921, 1926; and Eckenwalder, 1980a, b), and general biology (Chamberlain).

The work of Tang is remarkably complete, comprising aspects of pollination biology (1987a, b), seed dispersal and seedling survival (1989), and population structure as related to habitat (1991).

The distribution of West Indian and Floridian species of *Zamia* shows no discernible pattern and has been of little value in understanding the taxonomy of the genus in this area. When looking for explanations involving dispersal, one finds little information, and what is available supports neither long-distance dispersal in Florida nor inter-island dispersal. In independent studies, Eckenwalder (1980b) and Tang (1989) found that nearly 50 percent of *Z. integrifolia* seeds were found within 1 m of the parent plant, with only about 5 percent at distances greater than 4 m. Many of the seeds were within 15 cm of the parent plant (Tang, 1989). In fact one often finds many seeds actually germinating within the crown of leaves. Because, as Eckenwalder (1980b) pointed out, a distance of 4 m from the parent plant is beyond the range of gravitational dispersal for ground-level cones in an area of flat terrain, some animal agent would seem to be involved in these cases. Although such agents have not been observed, indirect evidence in the form of marks on the seeds and the affinity of mockingbirds for the seeds of related species growing at the Fairchild Tropical Garden indicates that birds and small mammals are involved in these dispersal events (Eckenwalder, 1980b; Tang, 1989). Further evidence comes from Tang's observation (1989) that most dispersed seeds are found under shrubs, rather than in exposed sunny areas, indicating bird-landing sites and areas where small mammals may have sought shelter. Tang also noted that most potential bird dispersers had a mouth-gape either less than the minimum diameter of the seeds or in some cases less than the median diameter. Thus, birds could only transport seeds a short distance before dropping them, which is consistent with the observed distribution of seeds beyond the parent plant. Beyond this, Eckenwalder (1980b) demonstrated the potential for inter-island dispersal. After two weeks of immersion in seawater, 92 percent of the seeds germinated and produced normal seedlings.

Seed germination and seedling survival were also studied under natural conditions by both Eckenwalder and Tang. Eckenwalder found that 97 percent of a sample of seeds germinated during the first year. However, only about 1 percent survived into the second year, demonstrating a very high seedling mortality. Tang obtained similar results. In a comparison of sun and shade areas, he found a 53 percent germination rate in the sun compared to an 85 percent germination rate in the shade. After 15 months, 22 percent of the seedlings germinated in the shade had survived, while only 5 percent of those in the sun were alive. It would thus appear that successful seedling establishment is enhanced by dispersal to shaded sites. Whereas shade conditions favor seedlings, Tang (1991) also showed reduced reproductive vigor in terms of smaller cone size and numbers of cones in plants in the shade. He found that cone production was significantly lowered after the understory vegetation had recovered from fire and shade was restored (Tang, 1991). The switch from a shade requirement for seedling establishment to a sun requirement for high cone production apparently is related to habitat. *Zamia integrifolia* is commonly found in pinelands that are (or were) subjected to periodic fires that open up the habitat by the destruction of shrubs. The underground contractile stem and roots of *Z. integrifolia* make it resistant to fire, and the opening up of the vegetation provides more light, which in turn allows more sunlight for cone production, especially for large ovulate cones with maturing seeds. Thus, this species is adapted for establishment in shade and for reproductive vigor after fire.

The seeds and/or stems of most neotropical cycads, including species of *Zamia*, are used as a source of starch for making breads and puddings. All plant parts, except the sarcotesta, are highly toxic and carcinogenic and must be thoroughly treated during processing to remove these components. The general method of starch extraction involves grating the stems and soaking the pulp in water to remove the toxins. The supernatant is then discarded and the recovered starch repeatedly washed to further remove toxic residues. Sturtevant provides an excellent discussion of this use of *Zamia* in the West Indies.

The best summary of the historical uses of *Zamia integrifolia* in Florida is that of Small (1921), who gives a list of common names used by native Americans. The two most in use were "conti" and "coontie." The underground stem was used as a source of starch after a detoxifying treatment. There appears to be good evidence that coontie was used in Florida as a staple before and after the arrival of the Seminoles. This would explain why *Z. integrifolia* is often found growing on shell middens in Florida (Small, 1921). Historically, *Zamia* has been used throughout the West Indies as a source of starch by Arawak Indians and others. In this may lie some answers to problems presented by the current distribution of *Zamia* in this area because the Arawaks traveled from island to island, perhaps transporting plants to use as food sources. Although conjectural, the variability of Florida populations may reflect repeated introductions by native Americans.

Early colonial settlers also used *Zamia integrifolia*, Florida arrowroot, as a source of starch and for the manufacture of arrowroot flour (Chamberlain; Small, 1921). During the nineteenth century, there were mills for the commercial production of arrowroot flour in South Florida; these had disappeared by the twentieth century. Although not now available as a commercial food, there has been some interesting use in this century. According to an elderly school teacher who was using a much worn copy of Britton and Millspaugh's "The Bahama Flora" (1920) and whom I met on a trip to Eleuthera in the Bahamas, *Zamia* was used as a staple food source by many Bahamian people during World War II when food supplies became scarce. In a similar vein, an elderly Jamaican woman recognized a potted *Zamia* plant in my home and told me that when she was a child her father maintained a plot of *Zamia* that they used to make sago pudding. She also said that during World War II many country people in Jamaica used the plant as a staple when food supplies became scarce as a result of shipping disruptions caused by the war. She believed that the plant was very rare in the wild in Jamaica as a result of over-exploitation during this period.

Zamia integrifolia is currently used as a horticultural ornamental in warmer climates and as a houseplant in colder ones. It is possible to purchase plants, generally wild collected ones, in many garden centers or plant shops in major cities in North America. It is ironic that this species is protected from international trade by CITES, but its commercial exploitation is not regulated in the United States.

REFERENCES:

- Under family references see AUDRAN & MASURE; DE CANDOLLE; CHAMBERLAIN; DEHGAN & DEHGAN; ECKENWALDER, 1980a, b; MARSHALL *et al.*; and STEVENSON, 1981, 1990a.
- FAWCETT, P., & K. NORSTOG. *Zamia pumila* in South Florida; a preliminary report on its pollinators *Rhopalotria slosoni*, a snout weevil, and *Pharaxonotha zamiae*, a clavicorn beetle. Proceedings of the Second International Conference on Cycad Biology, Palm and Cycad Society of Australia, Milton, Australia. (In press.) 1991.
- JOHNSON, M. A. Structure of the shoot apex in *Zamia*. Bot. Gaz. 101: 189-203. 1939.
- . Foliar development in *Zamia*. Am. Jour. Bot. 30: 366-378. 1943.
- MORETTI, A. Cytotaxonomy of cycads. Mem. New York Bot. Gard. 57: 114-122. 1990a. [Survey of 58 species in nine genera.]
- . Karyotypic data on North and Central American Zamiaceae (Cycadales) and their phylogenetic implications. Am. Jour. Bot. 77: 1016-1029. 1990b. [Four genera, including *Chigua*; 32 species.]
- & S. SABATO. Karyotype evolution by centromeric fission in *Zamia* (Cycadales). Pl. Syst. Evol. 146: 215-223. 1984.
- NORSTOG, K. Fine structure of the spermatozoid of *Zamia* with special reference to the flagellar apparatus. Am. Jour. Bot. 54: 831-840. 1967.
- . Fine structure of the spermatozoid of *Zamia*, observations on the microtubule system and related structures. Phytomorphology 18: 350-356. 1968.

- . Role of archegonial neck cells of *Zamia* and other cycads. *Ibid.* **22**: 125–130. 1972.
- . Fine structure of the spermatozoid of *Zamia*: the vierergruppe. *Am. Jour. Bot.* **61**: 449–456. 1974.
- . The motility of cycad spermatozoids in relation to structure and function. *Jour. Linn. Soc. Biol.* **7**(Suppl. 1): 135–142. 1975.
- . Chromosome numbers in *Zamia* (Cycadales). *Caryologia* **33**: 419–428. 1980. [Nine species.]
- . Karyotypes of *Zamia Chigua* (Cycadales). *Ibid.* **34**: 255–260. 1981.
- . The blepharoplast of *Zamia pumila* L. *Bot. Gaz.* **147**: 40–46. 1986.
- & P. FAWCETT. Insect-cycad symbiosis and its relationship to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). *Am. Jour. Bot.* **76**: 1380–1394. 1989.
- , D. STEVENSON, & K. NIKLAS. 1986. The role of weevils in the pollination of *Zamia furfuracea* L. f. (Zamiaceae). *Biotropica* **18**: 300–306. 1986.
- PELLMYR, O., W. TANG, I. GROTH, G. BERGSTROM, & L. THIEN. Cycad cone and angiosperm floral volatiles: inferences for the evolution of insect pollination. *Biochem. Syst. Ecol.* **19**: In press. 1991.
- REGEL, E. Die Cycadeen, deren Gattung und Arten. *Gartenflora* **25**: 140–144. 1876.
- SABATO, S. West Indian and South American cycads. *Mem. New York Bot. Gard.* **57**: 173–175. 1990.
- SMALL, J. K. Seminole bread — the conti, a history of the genus *Zamia* in Florida. *Jour. New York Bot. Gard.* **22**: 121–137. 1921.
- . Cycads. *Ibid.* **27**: 121–129. 1926. [General account of cycads with emphasis upon *Zamia* in Florida]
- . Manual of the southeastern flora. xxii + 1544 pp. New York. 1933. [*Zamia*.]
- SMITH, F. G. Morphology of the trunk and development of the microsporangium of cycads. *Bot. Gaz.* **43**: 187–204. 1907.
- . Development of the ovulate strobilus and young ovule of *Zamia floridana*. *Ibid.* **50**: 128–141. 1910.
- . Multiple cones in *Zamia floridana*. *Ibid.* **88**: 204–217. 1929.
- STEVENSON, D. W. Observations on stem and root contraction in cycads (Cycadales) with special reference to *Zamia pumila* L. *Bot. Jour. Linn. Soc.* **81**: 275–281. 1980a.
- . Radial growth in the Cycadales. *Am. Jour. Bot.* **67**: 465–475. 1980b.
- . Again the West Indian zamias. *Fairchild Trop. Gard. Bull.* **42**(3): 23–27. 1987a.
- . Comments on character distribution, taxonomy, and nomenclature of the genus *Zamia* in the West Indies and Mexico. *Encephalartos* **9**: 3–7. 1987b.
- . Strobilar ontogeny in the Cycadales. Pp. 205–244 in P. LEINS, S. TUCKER, & P. ENDRESS (eds.), *Aspects of floral development*. Berlin. 1988. [An account of vegetative and reproductive branching in cycads]
- STURTEVANT, W. History and ethnography of some West Indian starches. Pp. 177–199 in P. UCKO & G. DIMBLEBY (eds.), *The domestication and exploitation of plants and animals*. Chicago. 1969. [An excellent account of history of use of *Zamia* in the West Indies.]
- TANG, W. Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *Am. Jour. Bot.* **74**: 90–99. 1987a.
- . Heat production in cycad cones. *Bot. Gaz.* **148**: 165–174. 1987b.
- . Seed dispersal in the cycad *Zamia pumila* in Florida. *Canad. Jour. Bot.* **67**: 2066–2070. 1989.
- . Reproduction in the cycad *Zamia pumila* in a fire-climax habitat: an eight year study. *Bull. Torrey Bot. Club* **118**: In press. 1991.
- VOVIDES, A. Insect pollination of some Mexican cycads in their natural habitat. *Biotropica* **23**: In press. 1991.

- WALTERS, T., & D. DECKER-WALTERS. Patterns of allozyme diversity in the West Indian cycad *Zamia pumila* (Zamiaceae). *Am. Jour. Bot.* **78**: 436-445. 1991.
- WEBBER, H. Peculiar structures occurring in the pollen tube of *Zamia*. *Bot. Gaz.* **23**: 456-459. 1897a.
- . The development of antherozoids in *Zamia*. *Ibid.* **24**: 16-22. 1897b.
- . Notes on the fecundation of *Zamia* and the pollen tube apparatus of *Ginkgo*. *Ibid.* **24**: 225-235. 1897c.
- . Spermatogenesis and fecundation of *Zamia*. U.S. Dep. Agr. Pl. Indust. Bull. **2**: 1-92. 1901.

FINDING-LIST OF FAMILIES, KEYS, AND GENERA TREATED IN THIS VOLUME

Only a few synonyms (in italics), mostly of segregate genera recognized by J. K. Small, *Manual of the Southeastern Flora*, 1933, are included.

BORAGINACEAE

Family	1	Echium	137	Myosotis	159
Key to genera	41	Hackelia	104	Onosmodium	132
Amsinckia	98	Heliotropium	74	Plagiobothrys	95
Argusia	70	Lappula	108	<i>Schobera</i>	74
<i>Batschia</i>	119	<i>Lithococcus</i>	74	<i>Sebestena</i>	43
Borago	146	Lithospermum	119	Symphytum	149
Bourreria	59	<i>Lycopsis</i>	129	<i>Tiaridium</i>	74
Buglossoides	129	<i>Mallotonia</i>	70	Tournefortia	65
<i>Cochranea</i>	74	Mertensia	88	<i>Varronia</i>	43
Cordia	43	<i>Messerschmidia</i>	70		
Cynoglossum	112	<i>Myriopus</i>	65		

GRAMINEAE (POACEAE) tribe PANICEAE

Tribe	171	Echinochloa	254	Reimarochloa	290
Key to genera	194	Eriochloa	272	<i>Rhynchelytrum</i>	310
Alloteropsis	262	Hymenachne	250	Sacciolepis	252
Anthaenantia	196	Lasiacis	254	Setaria	294
Anthephora	220	<i>Leptoloma</i>	198	Stenotaphrum	307
Axonopus	291	Melinis	310	<i>Syntherisma</i>	198
<i>Brachiaria</i>	264	Oplismenus	222	<i>Trichachne</i>	198
Cenchrus	215	Panicum	224	Tricholaena	310
<i>Chaetochloa</i>	294	Paspalidium	305	Urochloa	264
<i>Dichanthelium</i>	224	Paspalum	277	<i>Valota</i>	198
Digitaria	198	Pennisetum	205		

PEDALIACEAE

Family	313	Ceratotheca	343	Sesamum	328
Key to genera	327				

PIPERACEAE

Family	349	<i>Micropiper</i>	357	Peperomia	357
Key	351	Piper	351	<i>Rhynchophorum</i>	357

ZAMIACEAE

Family	367	Zamia	371		
--------	-----	-------	-----	--	--

1385 120

CONTENTS OF SUPPLEMENTARY SERIES, VOLUME 1

The Genera of Boraginaceae in the Southeastern United States.

IHSAN A. AL-SHEHBAZ..... 1-169

The Genera of Paniceae (Gramineae: Panicoideae) in the Southeastern United States.

WILLIAM J. CRINS 171-312

The Genera of Pedaliaceae in the Southeastern United States.

STEPHEN D. MANNING 313-347

The Piperaceae in the Southeastern United States.

ALLAN J. BORNSTEIN 349-366

The Zamiaceae in the Southeastern United States.

DENNIS WM. STEVENSON 367-384

Edited by Carroll E. Wood, Jr. and Norton G. Miller



